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THE HYLID FROGS OF MIDDLE AMERICA



THE HYLID FROGS  
OF  
MIDDLE AMERICA

VOLUME 2

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### The *Hyla bromeliacia* Group

**DEFINITION:** The members of this group are small bromeliad inhabitants; males attain a maximum snout-vent length of 31.6 mm. and females, 34.6 mm. The dorsum is yellow or tan without distinctive markings. The palpebral membrane is clear. The fingers are no more than one-third webbed, and the toes are about two-thirds webbed. Dermal fringes and appendages are lacking on the limbs, and a distinct axillary membrane is present. Males have single, median, subgular vocal sacs and horny nuptial excreseences on the pollicies. The cranial elements are not extensively ossified; a large frontoparietal fontanelle is present (fig. 220). The sphenethmoid is short and barely extends anteriorly to the nasals, which are long and slender, broadly separated medially, and not sutured to the sphenethmoid. The anterior end of the sphenethmoid is truncate and entirely behind the nasals (*bromeliacia*) or notched anteriorly and overlain by the posteromedial corner of each nasal (*dendroscarta*). The quadratojugal is absent (*bromeliacia*) or present (*dendroscarta*). The anterior arm of the squamosal extends only about one-third of the distance to the maxillary, and the squamosal is not in bony contact with the erista parotica. The medial ramus of the pterygoid does not have a bony articulation with the prootic. Prevomerine teeth are present. The tadpoles have long muscular tails with rudimentary fins and small ventral mouths with two upper and four or five lower rows of teeth. The known mating call consists of a short series of quickly repeated notes. The number of chromosomes is unknown.

**COMPOSITION:** Two species (*Hyla bromeliacia* and *dendroscarta*) comprise the group, which occurs in cloud forests on the Atlantic slopes of México and northern Central America. Of the two species, 257 preserved frogs, two skeletons, eight lots of tadpoles, and one preserved clutch of eggs have been examined.

**COMMENTS:** The two species in this group are alike in having vocal slits extending posterolaterally from the posterolateral edges of the tongue, which is not free posteriorly. The crania are alike in having small, slender nasals. The tadpoles of the species in the *Hyla bromeliacia* group are nearly indis-

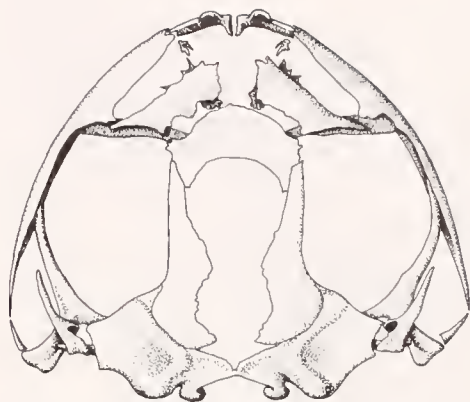


FIG. 220. Dorsal view of the skull of *Hyla bromeliacia*, K.U. No. 59888.  $\times 6$ .

tinguishable from one another but are strikingly different from any other Middle American hylid tadpoles. There is little doubt but what *Hyla bromeliacia* and *dendroscarta* are closely related, perhaps conspecific.

On the basis of cranial characters, members of this group might be related to *Hyla miotympanum*, but the minor differences and many similarities in cranial features of the various small stream-breeding *Hyla* in México, together with the specialized tadpoles of the *Hyla bromeliacia* group makes this possible alliance tenuous.

### *Hyla bromeliacia* Schmidt

*Hyla bromeliacia* Schmidt, 1933b, p. 19 [holotype, F.M.N.H. No. 4718 from the mountains west of San Pedro Sula, Departamento Cortés, Honduras; Karl P. Schmidt and Leon L. Walters collectors]. Stuart, 1963, p. 35.

**DIAGNOSIS:** This small yellowish tan species has an acutely rounded snout in dorsal profile, an axillary membrane and no distinctive markings. It can be distinguished from its apparent nearest relative, *dendroscarta*, by having pigmented ventral surfaces of the hands and feet, suffusion of dark pigment on the throat, more blunt snout, and proportionately shorter hind limbs (the mean ratio of tibia length to snout-vent length is 0.506 in *bromeliacia* and 0.559 in *dendroscarta*). The only other *Hyla* in northern Middle America with which *bromeliacia* might be confused is *sumichrasti*; the latter has an indistinct tympanum, pointed snout, and no tarsal fold.



**DESCRIPTION:** Males of this small species attain a maximum snout-vent length of 29.5 mm., and females reach 32.7 mm. In a series of six males from the Atlantic slopes of central Guatemala, the snout-vent length is 24.1 to 29.5 (mean, 27.0) mm.; the ratio of tibia length to snout-vent length is 0.488 to 0.532 (mean, 0.506); the ratio of foot length to snout-vent length is 0.413 to 0.436 (mean, 0.425); the ratio of head length to snout-vent length is 0.341 to 0.372 (mean, 0.357); the ratio of head width to snout-vent length is 0.344 to 0.372 (mean, 0.355), and the ratio of the diameter of the tympanum to that of the eye is 0.410 to 0.563 (mean, 0.493). Two females from the same area have snout-vent lengths of 32.0 and 32.7 mm. In these specimens, the ratio of the diameter of the tympanum to that of the eye is 0.381 and 0.410.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is acutely rounded; in lateral profile, it is bluntly rounded. The snout is moderately long; the nostrils are barely protuberant and situated at a point about three fourths of the distance from the eyes to the tip of the snout. The canthus is weakly angular; the loreal region is barely concave, and the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold barely obscures the upper edge of the tympanum, which otherwise is distinct and is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately short and robust; an abbreviated axillary membrane is present. A low, indistinct row of tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are moderately short and stout and bear large discs; the width of the disc on the third finger is equal to the diameter of the eye. The subarticular tubercles are moderately large and flattened; the distal one on the fourth finger is noticeably bifid. The supernumerary tubercles are large and subconical; they are especially numerous on the proximal segment of the third finger. The palmar tubercle is

large, flat, and bifid. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrecence. The fingers are about one-fourth webbed (fig. 221A). The webbing is vestigial between the first and second finger, and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and stout; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. The heel is tubercular and bears a heavy transverse dermal fold. The tarsal fold is low, indistinct, and extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, elliptical, and noticeably visible from above. The outer metatarsal tubercle is small and subconical. The toes are moderately long and robust and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are large and round. The toes are about two-thirds webbed (fig. 221C). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth, and from the middle of the antepenultimate phalanx of the fourth to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally near the midlevel of the thighs. A short anal sheath is present, and large tubercles are present below the anal opening. The skin on the dorsum and on the ventral surfaces of the arms and shanks is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. The tongue is narrowly cordiform, barely notched posteriorly, and not free behind. The dentigerous processes of the prevomers are moderately small, wide-

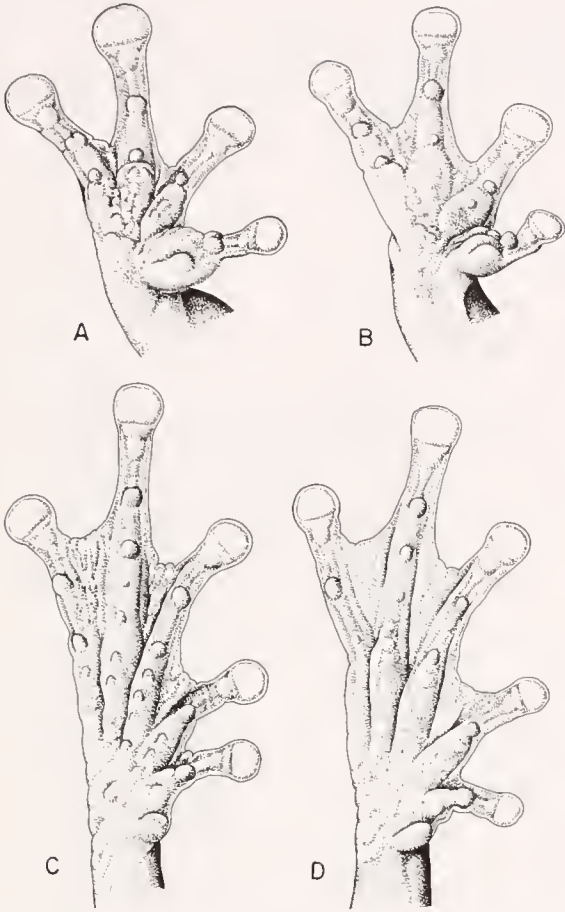


FIG. 221. Hands and feet of members of the *Hyla bromeliacia* group. A and C. *Hyla bromeliacia*, K.U. No. 57249. B and D. *Hyla dendroscarta*, U.M.M.Z. No. 118167.  $\times 5$ .

ly separated, elliptical ridges between the moderately large ovoid choanae. There are three or four teeth on each prevomerine process. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla bromeliacia* is pale brown or yellowish tan with no distinctive dorsal markings (pl. 59, fig. 5). The flanks and anterior and posterior surfaces of the thighs are pale pinkish tan; the ventral surfaces of the hind limbs are dull yellow and the venter is white. In some specimens, a faint white anal stripe is evident. The iris is a dull bronze with small black flecks.

Most individuals when found in bromeliads by day were brown; later, these changed to pale tan. Individuals that were active at night were pale tan above. A few minute dark flecks or whitish flecks are present on the dorsum; otherwise, there are no markings.

In preservative, the dorsum varies from dull tan to brown with or without minute darker flecks. The flanks, upper surfaces of the first two toes, and the anterior and posterior surfaces of the thighs are tan. The venter is creamy tan. There is a suffusion of dusty brown pigment on the throat, and the ventral surfaces of the hands and feet are pigmented with brown; this is especially evident on the supernumerary tubercles on the feet.

**TADPOLES:** A typical tadpole in developmental stage 35 has a body length of 9.3 mm. and a total length of 31.0 mm. The body is greatly depressed; it is nearly twice as wide as deep and is widest posteriorly. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is acutely rounded and nearly spatulate. The eyes are small, widely separated, and directed laterally. The nostril is directed anteriorly at a point somewhat closer to the tip of the snout than to the eye. The opening in the sinistral spiracle is at a point on the midline about two-thirds of the distance from the tip of the snout to the posterior end of the body. The anal tube is moderately long and dextral. The caudal musculature is massive and extends nearly to the end of the rounded tail. The fins are very shallow; they are deepest posteriorly, and the dorsal fin does not reach to the body (fig. 222A).

The tadpoles are dull tan to creamy brown above. The venter is transparent, so that the heart is clearly visible. In preservative, they are pale creamy tan with black flecks on the dorsum of the body and on the caudal musculature. The fins are transparent.

The mouth is ventral and small; its width is less than one-half of the greatest width of the body. There is no lateral fold and the upper lip is bare. Two rows of small papillae are present on the lower lip. The beaks are massive and bear moderately long, pointed



FIG. 222. Tadpoles of members of the *Hyla bromeliacia* group. A. *Hyla bromeliacia*, K.U. No. 59980. B. *Hyla dendroscarta*, K.U. No. 104129.  $\times 4$ .

serrations. The upper beak forms a broad arch with short lateral processes; the lower beak forms a narrow arch. There are two upper and four or five lower rows of teeth. The upper rows are long and extend nearly to the lip. The second upper row is narrowly interrupted medially. The lower rows are progressively shorter from the first to the fifth; all are complete. The fifth row, when present, usually is fully developed (fig. 223A).

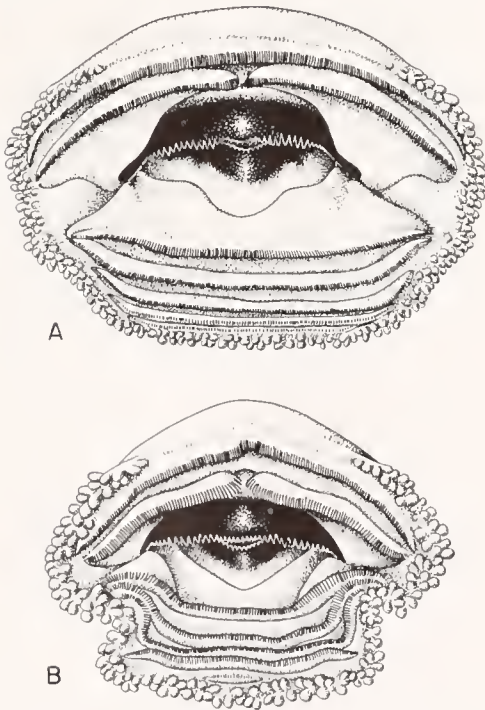


FIG. 223. Mouths of tadpoles of members of the *Hyla bromeliacia* group. A. *Hyla bromeliacia*, K.U. No. 59980. B. *Hyla dendroscarta*, K.U. No. 104129.  $\times 20$ .

The preceding description of tadpoles from Finca Chicoyou, Alta Verapaz, Guatemala, indicates that the tadpoles that I collected there are identical to those described by Stuart (1948, p. 30) from the nearby Finca Samac.

Hatchling tadpoles (developmental stage 21) have body lengths of 2.5 to 2.7 mm. and total lengths of 6.7 to 7.1 mm. A good developmental series of tadpoles was obtained at Finca Chicoyou (table 40). Of those specimens assignable to developmental stage 25, there are two size-groups. The maximum body length in the first group is 5.7 mm., whereas the minimal body length in the second group is 7.0 mm., and the entire range in size in developmental stage 25 is 3.8 to 9.0 mm. The two size-groups are differentiated on the basis of the development of the teeth. In the smaller group, there are only four lower rows of teeth and the fourth row is weakly developed; in some specimens, the third row is also poorly developed. In the larger specimen, a fifth tooth row is present in most individuals, but some have only four rows; in these, the fourth row is well developed.

**MATING CALL:** The mating call of *Hyla bromeliacia* consists of five or six soft notes repeated at intervals of 45 to 70 seconds. The duration of each call group is approximately five seconds. The last note in each call group is double or triple in some calls. The analysis of one recording shows that each note has a duration of about 0.14 of a second; the pulse rate is approximately 195 pulses per second. The fundamental frequency is about 135 cycles per second, and the dominant



TABLE 40  
Measurements of Tadpoles, with Means in Parentheses,  
in Relation to Developmental Stages in *Hyla bromeliacia*.

Stage	N	Body Length	Tail Length	Total Length
21	2	2.5-2.7 (2.6)	4.2-4.4 (4.3)	6.7-7.1 (6.9)
25A	7	3.8-5.7 (4.8)	9.0-13.5 (11.4)	12.8-19.2 (15.9)
25B	10	7.0-9.0 (8.0)	16.7-22.0 (19.1)	23.7-29.5 (27.1)
28	8	8.3-9.2 (8.7)	20.2-22.2 (21.0)	28.9-31.0 (29.7)
31	1	9.3	21.0	30.3
35	2	9.3-9.7 (9.5)	21.5-21.7 (21.6)	31.0-31.2 (31.1)
37	2	9.0-9.5 (9.3)	21.0-21.5 (21.3)	30.0-31.0 (30.5)
39	3	9.0-9.5 (9.3)	19.7-21.6 (20.9)	28.7-31.0 (30.2)
41	2	10.3-10.5 (10.4)	20.0-20.2 (20.1)	30.5
46	2	11.1-11.5 (11.3)	-----	-----

frequency is about 3100 cycles per second (pl. 18, fig. 1).

**NATURAL HISTORY:** *Hyla bromeliacia* is an inhabitant of cloud forests, where it lives in bromeliads. This small species deposits its eggs in the water at the bases of the leaves of the bromeliads, and the tadpoles undergo their development in the bromeliads. Schmidt (1933b, p. 19) reported eggs in the bromeliads in the Sierra de Merendón in Honduras, and Stuart (1943, p. 14) reported eggs in bromeliads in the Sierra de los Cuchumantanes in Guatemala. The latter author stated: "These [the eggs] lay between the leaves and numbered about a dozen to a cluster. They were enclosed in gelatin capsules and were loosely held together (roughly in pairs) by very watery gelatin." At Finca Chieoyou, Departamento Alta Verapaz, Guatemala, on July 17, 1960, I found one clutch of 14 eggs that were adherent to the leaves of a bromeliad, just below the surface of the water (pl. 8, fig. 3).

The tadpoles wriggle about in the water at the bases of the leaves in the bromeliads and are capable of moving over the wet surfaces of leaves out of the water by violent wiggling of the long muscular tail.

Stuart (1948b, p. 31) noted that the breeding season probably extends throughout the year. In April, 1938, he found eggs as well as tadpoles in varying stages of development. In July, 1960, I also obtained eggs and tadpoles in all stages of development, as well as metamorphosing young. Young individuals having snout-vent lengths of 11.1 and 11.5 mm. were found in bromeliads; these small individuals were colored like the adults. A somewhat larger young, having a snout-vent length of 15.5 mm. was found on a tree limb at night.

Males call from bromeliads or infrequently from leaves or branches of trees. The bromeliads cause a directional influence on the call; furthermore, the call is extremely soft in this small species. Consequently, calling males are extremely difficult to locate.

**REMARKS:** It is interesting to note that the bromeliad tadpoles of *Hyla bromeliacia* and the related *Hyla dendroscarta* are alike in having well developed rows of teeth and beaks. The only other known bromeliad tadpole of the genus *Hyla* in Middle America is that of *Hyla zeteki* (Dunn, 1937; Starrett, 1960a). The tadpole of *Hyla zeteki* has an anterodorsal mouth with poorly developed

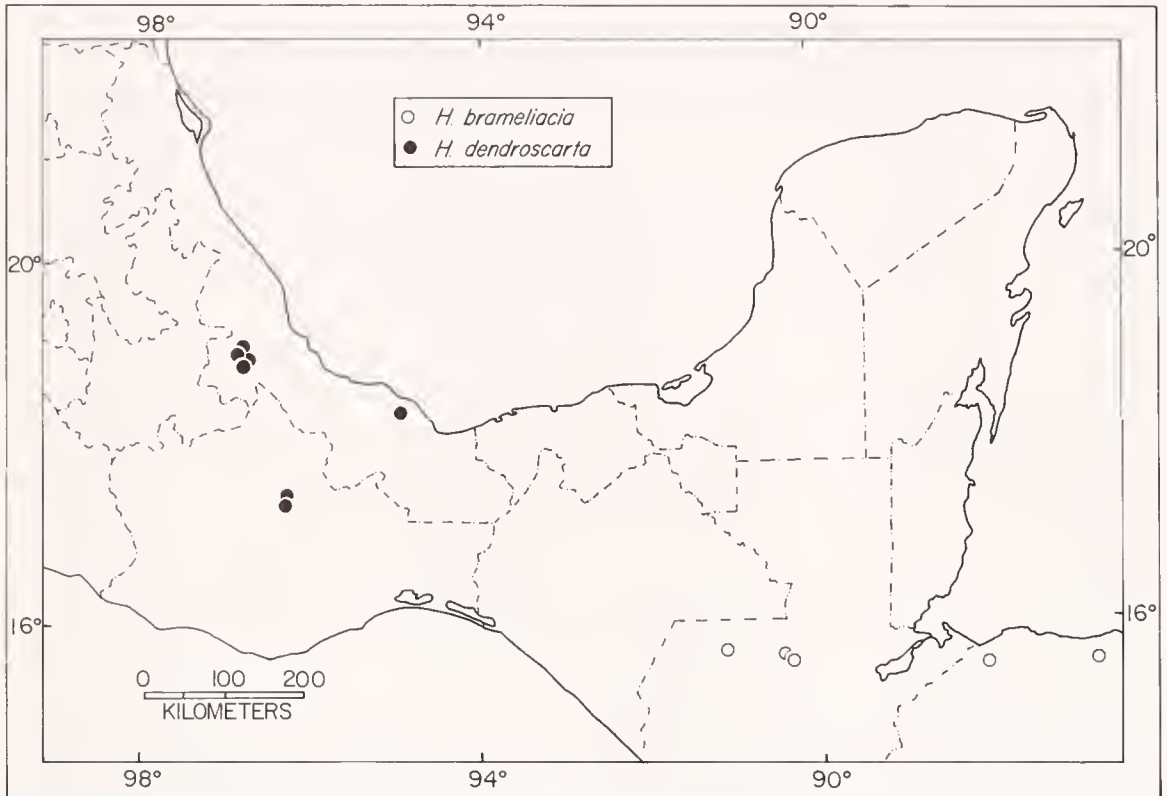


FIG. 224. Distribution of *Hyla bromeliacia* and *Hyla dendroscarta*.

teeth. Furthermore, the body is not especially depressed, nor is the tail especially long. The shape of the body in *Hyla bromeliacia* and *dendroscarta* is like that of the bromeliad tadpoles of the Jamaican hylids (*H. brunnea*, *lichenata*, *marianuae*, and *wilderdae*); however, the tadpoles of the Jamaican species have greatly reduced mouthparts (Dunn, 1926).

**ETYMOLOGY:** The specific name is derived from the Latin *bromelia*, a generic name for a group of epiphytic bromeliads, and the Latin *aceus*, meaning belonging to, and refers to the bromeliad habitat of this species.

**DISTRIBUTION:** *Hyla bromeliacia* occurs at elevations of 900 to 1300 meters on the Atlantic slopes of northern Central America from the Sierra de los Cuchumatanes in western Guatemala to the Sierra de Nombre de Dios in north-central Honduras (fig. 224).

See Appendix 1 for the locality records of the 27 specimens examined.

### *Hyla dendroscarta* Taylor

*Hyla dendroscarta* Taylor, 1940b, p. 45 [holotype, U.S.N.M. No. 108679 from Cuautlapam, Veracruz, México; Hobart M. Smith collector]. Smith and Taylor, 1948, p. 89.

**DIAGNOSIS:** This small yellow species has a pointed snout in dorsal profile, an axillary membrane, and no distinctive markings. It can be distinguished from the related *bromeliacia* by having a pointed, instead of acutely rounded snout, lacking dark pigment on the throat and ventral surfaces of the hands and feet, and by having proportionately longer hind limbs (the mean ratio of tibia length to snout-vent length is 0.559 in *dendroscarta* and 0.506 in *bromeliacia*). *Hyla dendroscarta* resembles *sunichrasti*, but the latter is easily distinguished by its weakly defined tympanum and absence of a tarsal fold.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 31.6 mm., and females reach 34.6 mm. In a series of



10 males from Cuautlapam, Veracruz, México, the snout-vent length is 27.2 to 29.8 (mean, 28.1) mm.; the ratio of tibia length to snout-vent length is 0.534 to 0.591 (mean, 0.559); the ratio of foot length to snout-vent length is 0.417 to 0.445 (mean, 0.424); the ratio of head length to snout-vent length is 0.326 to 0.360 (mean, 0.347); the ratio of head width to snout-vent length is 0.342 to 0.367 (mean, 0.358), and the ratio of the diameter of the tympanum to that of the eye is 0.375 to 0.452 (mean, 0.410). A single female from the same locality has a snout-vent length of 33.6 mm., whereas four females from the north slope of the Sierra de Juárez in Oaxaca have snout-vent lengths of 32.7 to 34.6 (mean, 33.4) mm. In 23 males from the Sierra de los Tuxtlas in southern Veracruz, México, the snout-vent length is 26.3 to 31.6 (mean, 28.4) mm. The proportions do not show significant variation in the different samples.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is pointed; in lateral profile, it is truncate and rounded above. The snout is moderately long; the nostrils are slightly protuberant at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is barely angular; the loreal region is nearly flat and sloping to the moderately thickened and slightly flared lips. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arms are moderately short and robust; an abbreviated axillary membrane is present. No distinctive row of tubercles is present on the ventrolateral edge of the forearm, but a weak, transverse dermal fold is present on the wrist. The fingers are moderately short and bear moderately small discs; the width of the disc on the third finger is slightly less than the diameter of the tympanum. The subarticular tubercles are large and subconical; in some specimens, the distal tubercle on the fourth finger is barely bifid. The supernumerary tubercles are small and subconical; they

are especially numerous on the proximal segment of the third finger. The palmar tubercle is small and subconical. The prepollex is moderately enlarged and in breeding males bears a weak nuptial excrescence. The fingers are about one-third webbed (fig. 221B). The webbing is vestigial between the first and second fingers, but extends from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and from the distal end of the antepenultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short, but not robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A thin, transverse dermal fold is present on the heel, and a weak, interrupted in some specimens, tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately small, flat, elliptical, and barely visible from above. A distinct outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are barely evident. The toes are about two-thirds webbed (fig. 221D). The webbing extends from the distal end of the antepenultimate phalanx of the first toe to the middle of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth, and from the distal end of the antepenultimate phalanx of the fourth to the distal end of the antepenultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the midlevel of the thighs. A moderately long anal sheath is present. Numerous small tubercles are present below the anal opening. The skin on the throat, belly, and posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is cordiform, very shallowly notched posteriorly, and not free behind. The dentigerous pro-

cesses of the prevomers are small, transverse or anteromedially inclined, widely separated elevations between the large, ovoid choanae. There are three to five teeth on each prevomerine process. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla dendroscarta* is yellow or pale yellowish tan with no markings (pl. 59, fig. 6). The entire dorsal surfaces are uniform yellowish tan, except in a few specimens in which faint darker tan flecks or transverse dashes are present on the back. The anterior and posterior surfaces of the thighs are yellow, and the flanks are creamy yellow. The throat and belly are white, and the iris is golden bronze with faint black reticulations.

In preservative, the dorsum is pale creamy tan with minute dark flecks, the venter is uniform creamy white. The tissues between the maxillary and premaxillary teeth is pigmented.

**TADPOLES:** A typical tadpole in developmental stage 25 has a body length of 9.7 mm. and a total length of 31.0 mm. The body is noticeably depressed; it is about half again as wide as deep. The body is slightly wider posteriorly than anteriorly. In dorsal profile, the snout slopes anteroventrally from the eye to an acutely rounded tip. The eyes are small, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about two-thirds of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline and slightly posterior to the midlength of the body. The anal tube is moderately short and dextral. The caudal musculature is massive and extends nearly to the tip of the long, pointed tail. The caudal fins are very shallow, slightly deeper posteriorly, and noticeably shallower than the caudal musculature; the dorsal fin does not extend on to the body (fig. 222B).

The dorsal part of the body and the caudal musculature are pale creamy tan; the venter is transparent. In preservative, the entire tadpole, with the exception of the transparent venter is white, except for a few

minute dark flecks on the dorsal part of the caudal musculature.

The mouth is ventral and small; its width is equal to about one-half of the greatest width of the body. A shallow, lateral fold is present in the lip. Except laterally, the upper lip is bare; the lower lip bears two rows of small papillae. Additional small papillae are present lateral to the teeth. The beaks are relatively heavy and bear short, pointed serrations. The upper beak is in the form of a broad arch with short, robust lateral processes; the lower beak also is arch-shaped. There are two upper and four lower rows of teeth. The upper rows are long and extend laterally to the edge of the lip. The second upper row is narrowly interrupted medially. All lower rows are continuous, and the first three lower rows are about equal in length and nearly as long as the upper rows, whereas the fourth lower row is noticeably shorter and less well developed (fig. 223B).

These tadpoles from Mirador, Veracruz, agree with the description of tadpoles from Cuautlapam, Veracruz, given by Taylor (1940, p. 47).

**MATING CALL:** The presence of vocal slits and a vocal sac suggest that this species has a call, but to my knowledge the call is unknown.

**NATURAL HISTORY:** *Hyla dendroscarta* inhabits cloud forest where apparently it breeds throughout the year. The eggs are deposited in the water in bromeliads, and the tadpoles develop in bromeliads. Taylor (1940b, p. 47) noted tadpoles in various developmental stages and eggs at Cuautlapam, Veracruz, on August 18, 1939. I have found tadpoles of this species in bromeliads at Mirador and near Huatusco, Veracruz, in January, February, and August.

**REMARKS:** The specimens from the vicinity of San Andrés Tuxtla, Veracruz (K.U. Nos. 23877 and 23879-23902), are poorly preserved and formalin-blackened. Although in those structural features that can be ascertained, the specimens most closely fit *Hyla dendroscarta*. I am not certain that they belong with this species.

**ETYMOLOGY:** The specific name is derived from the Greek *dendron*, meaning tree, and the Greek *skartes*, meaning nimble or quick,

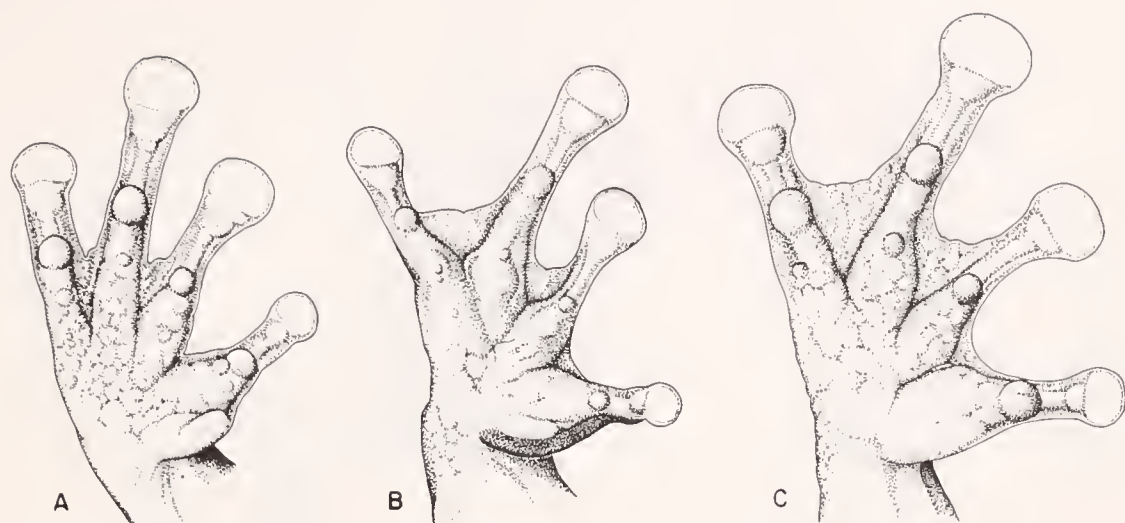


FIG. 225. Hands of species in the *Hyla taeniopus* group. A. *H. chaneque*, K.U. No. 58439. B. *H. taeniopus*, K.U. No. 53834. C. *H. altipotens*, K.U. No. 101001.  $\times 3$ .

and alludes to the arboreal habits of this bromeliad inhabitant.

**DISTRIBUTION:** *Hyla dendroscarta* occurs on the Atlantic slopes of the Sierra Madre Oriental and associated mountain ranges from central Veraeruz to northern Oaxaca, and in the Sierra de los Tuxtlas in southern Veraeruz, México (fig. 224); the species is known from elevations of 450 to 1900 meters.

See Appendix 1 for the locality records of the 241 specimens examined.

#### The *Hyla taeniopus* Group

**DEFINITION:** The members of this group are large species; males attain a maximum snout-vent length of 75 mm. and females, 80 mm. The dorsum is green or brown with darker blotches or spots and distinct transverse bands on the limbs. The palpebral membrane is clear. The fingers are one-half to two-thirds webbed, and the toes are about three-fourths webbed (figs. 225 and 226). A tarsal fold is present, but dermal appendages and fringes and an axillary membrane are absent. The anal sheath is long. Vocal slits are present or absent; in those species having vocal slits the vocal sac is single, median, subgular, and barely distensible. Nuptial excreseences are present on the polliices in some species and apparently lacking in one species (*altipotens*). The skulls are broad

and flat and have a long, narrow frontoparietal fontanelle (fig. 227). The nasals are broad and flat and have long, slender maxillary processes. The quadratojugals are well ossified and in bony contact with the maxillaries. The anterior arm of the squamosal is short and does not extend to the maxillary. Prevoomerine teeth are present. The tadpoles have small, ventral mouths with two upper and three or four lower rows of teeth; the tail is long and muscular, and iridophores and xanthophores (in some species) are present (figs. 228 and 229). The mating call (known only in *chaneque*) is a short, low-pitched groan. Males of *altipotens* and *taeniopus* have greatly enlarged testes. The haploid number of chromosomes is 12 (known only in *chaneque*).

**COMPOSITION:** Three species comprise the group.<sup>12</sup> *Hyla altipotens* and *taeniopus* occur on the Pacific and Atlantic slopes of the Mexican highlands, respectively; *chaneque* occurs on the Pacific slopes of the Chiapan highlands and on the Atlantic slopes of the Mexican and Chiapan highlands. Of the three

<sup>12</sup> In December, 1969, Dr. Kraig Adler, Mr. David M. Dennis, and Mr. David Snyder obtained a series of frogs belonging to this group from the Sierra Madre del Sur in Guerrero. cursory examination of these specimens suggests that they represent a previously undescribed species related to *H. altipotens* and *taeniopus*.



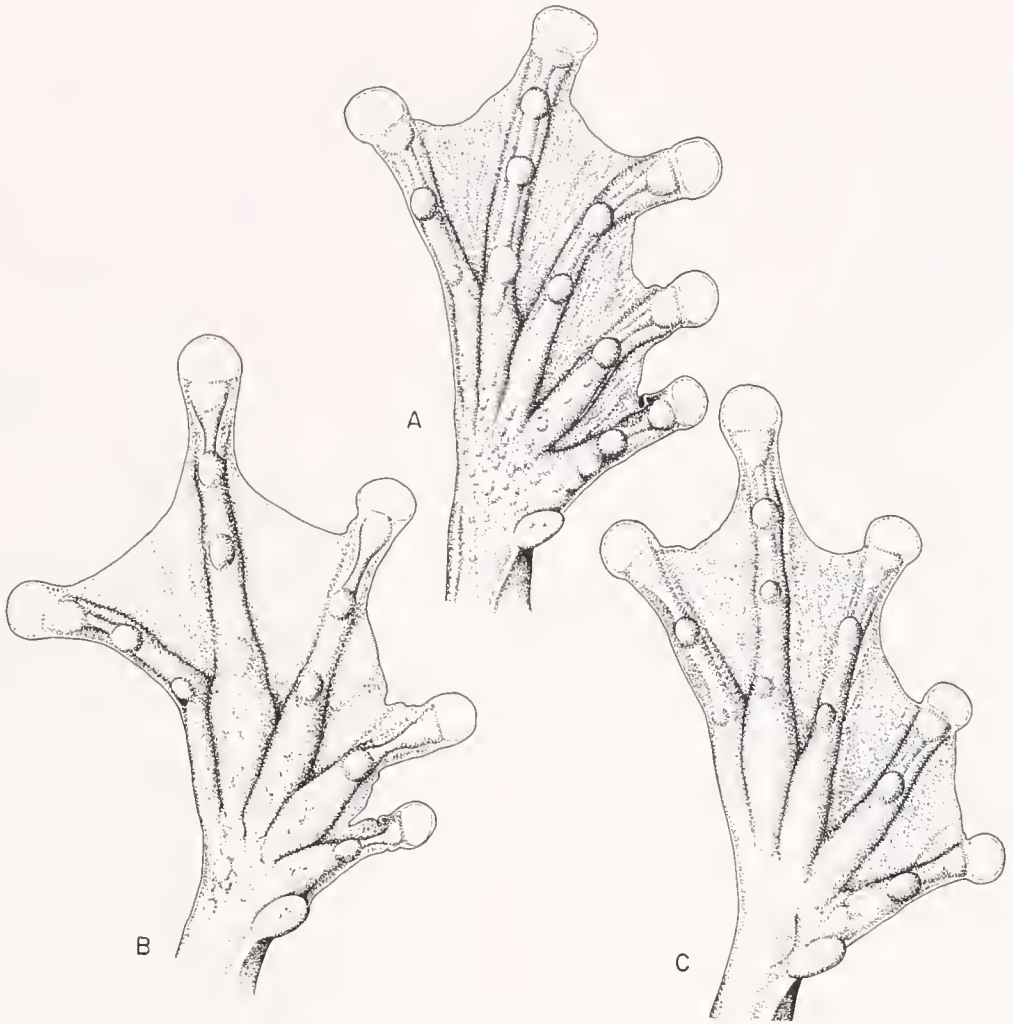


FIG. 226. Feet of species in the *Hyla taeniopus* group. A. *H. chaneque*, K.U. No. 58439. B. *H. taeniopus*, K.U. No. 53834. C. *H. altipotens*, K.U. No. 101001.  $\times 3$ .

species, 143 preserved frogs, 13 skeletons, and 12 lots of tadpoles have been examined.

COMMENTS: Some differences in measurements and proportions exist (table 41). *Hyla altipotens* is notably different from the other species by having a narrower head and longer legs. Within the *taeniopus* group, *chaneque* is the least advanced species. It has an unmodified (blunt) snout and not greatly enlarged testes; vocal slits are present in some specimens. *Hyla taeniopus* has minute vocal slits and possibly lacks a voice; *altipotens* lacks vocal slits. Both *altipotens* and *taeniopus* have greatly enlarged testes. In *taeniopus*, females have a blunt snout, where-

as males have a pointed, protruding snout; in *altipotens*, the snout is pointed in both sexes. All members of the group live in cloud forests, and the tadpoles develop in mountain streams.

The three species included in the *taeniopus* group comprise a series of taxa showing progressive modifications for life in and along mountain streams. In some respects (tadpoles and enlarged testes), these species have surpassed members of the *Hyla bistincta* group and the genus *Plectrohyla*, but in other aspects, such as degeneration of voice, they are no more advanced than members of those groups.

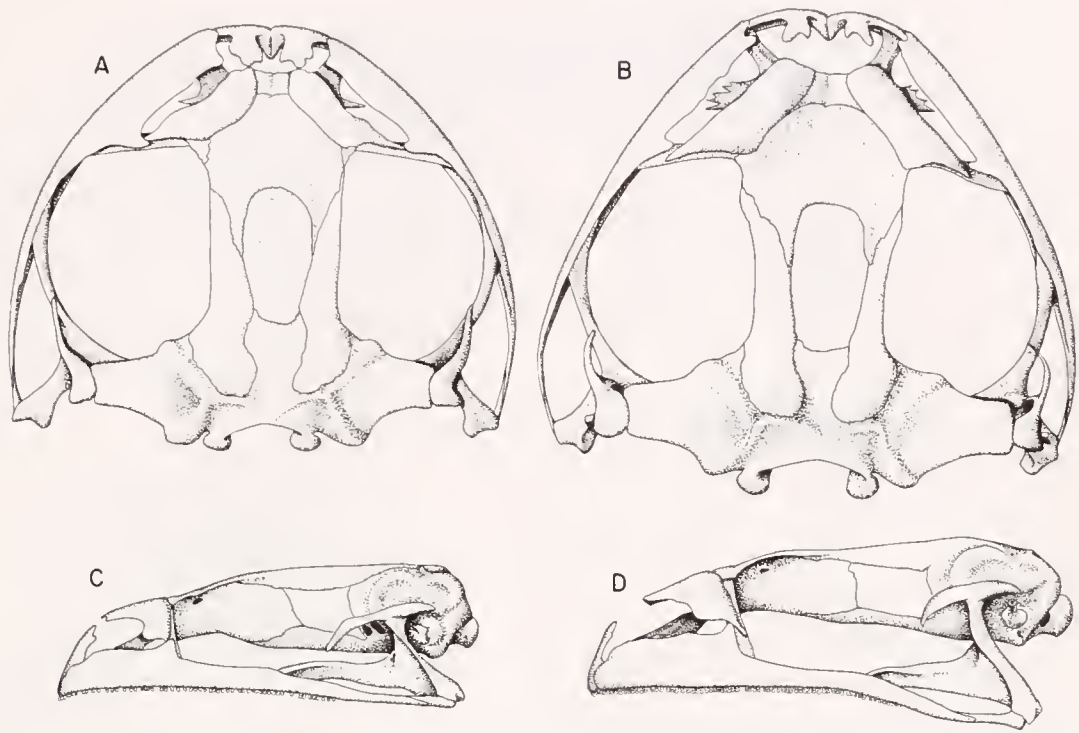


FIG. 227. Skulls of species in the *Hyla taeniopus* group. A and C. *H. chaneque*, K.U. No. 84907. B and D. *H. altipotens*, K.U. No. 104342.  $\times 5$ .

TABLE 41

Geographic Variation in Size and Certain Proportions, with Means in Parentheses, of the Species in the *Hyla taeniopus* Group.

Species	Sex	N	Snout-vent Length	Tibia Length/ S-V L	Head Length/ S-V L	Tympanum/ Eye
<i>H. chaneque</i> .....	♂	28	52.0-70.9 (57.5)	0.460-0.531 (0.489)	0.313-0.350 (0.331)	0.338-0.560 (0.448)
	♀	6	66.4-79.3 (71.8)	0.473-0.560 (0.509)	0.312-0.347 (0.325)	0.426-0.493 (0.452)
<i>H. taeniopus</i> .....	♂	18	48.0-65.9 (58.0)	0.450-0.500 (0.480)	0.290-0.340 (0.310)	0.510-0.620 (0.560)
	♀	8	56.6-70.0 (64.2)	0.470-0.520 (0.490)	0.300-0.330 (0.320)	0.540-0.660 (0.620)
<i>H. altipotens</i> .....	♂	5	68.8-75.1 (70.7)	0.526-0.558 (0.537)	0.281-0.300 (0.292)	0.414-0.552 (0.506)
	♀	2	69.4-75.3 (72.4)	0.558-0.562 (0.560)	0.288-0.311 (0.299)	0.533-0.630 (0.588)



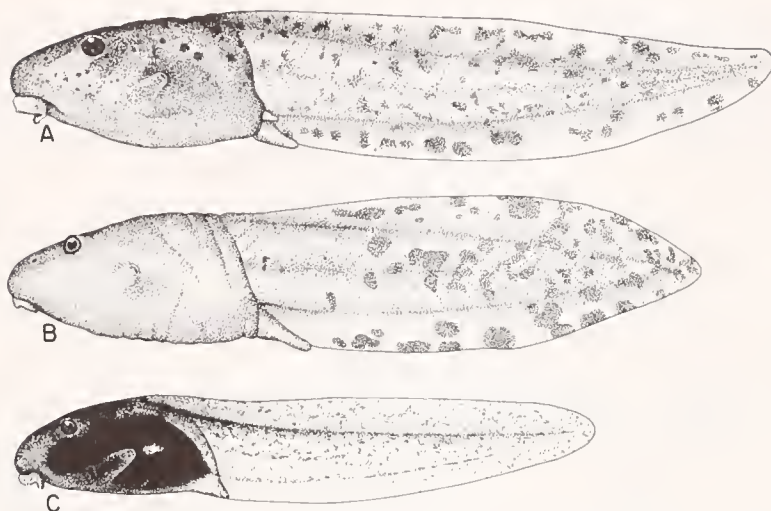


FIG. 228. Tadpoles of species in the *Hyla taeniopus* group. A. *H. chaneque*, K.U. No. 104124. B. *H. taeniopus*, K.U. No. 68498. C. *H. altipotens*, K.U. No. 104182.  $\times 2$ .

### *Hyla chaneque* Duellman

*Hyla chaneque* Duellman, 1961a, p. 1 [holotype, K.U. No. 58439 from a stream above (6.2 kilometers south of) Rayón Mescalapa, Chiapas, México, elevation 1690 meters; William E. Duellman collector]; 1965b, p. 164.

*Hyla duellmani* Lynch and Smith, 1966, p. 60 [holotype, U.I.M.N.H. No. 56821 from the Sierra Madre north of Zanatepec, Oaxaca, México, elevation about 1550 meters; Thomas MacDougall collector].

**DIAGNOSIS:** *Hyla chaneque* is a large tree frog (males attain a snout-vent length of 71 mm. and females, 80 mm.) having a green or brown dorsum, with darker green or brown blotches on the body, and transverse bands on the limbs. The venter is creamy tan or dark brown with or without dark spots on the chin. *Hyla chaneque* differs from other members of the *taeniopus* group by having a truncate snout in both sexes, a tuberculate dorsum, and a small tympanum, the diameter of which is usually less than half of the diameter of the eye. *Hyla altipotens* and *taeniopus* have smooth skin on the dorsum; the snout is acuminate in both sexes in *altipotens* and in males of *taeniopus*. The only other frog in northern Middle America that might be confused with *chaneque* is *Smilisca baudinii*; the latter has a smooth dorsum, pale creamy white belly, a much larger tympanum, and a dark postorbital mark.

**DESCRIPTION:** This is the largest species in the *Hyla taeniopus* group. Males attain a maximum snout-vent length of 74.9 mm., and females a maximum snout-vent length of 79.3 mm. In a sample of 23 males from the north slope of the Sierra de Juárez in northern Oaxaca, México, the snout-vent length is 52.0 to 70.9 (mean, 57.4) mm.; the ratio of tibia length to snout-vent length 0.460 to 0.531 (mean, 0.489); the ratio of foot length to snout-vent length is 0.424 to 0.485 (mean, 0.454); the ratio of head length to snout-vent length is 0.313 to 0.350 (mean, 0.332); the ratio of head width to snout-vent length is 0.333 to 0.369 (mean, 0.349), and the diameter of the tympanum to that of the eye is 0.338 to 0.560 (mean, 0.451). In five females from the same locality, the snout-vent length is 66.4 to 74.9 (mean, 70.0) mm. There are no significant differences between the sexes in proportions. Likewise, there is little difference in size or in proportions in specimens from throughout the range of the species (table 42). The discrepancy in maximum size of individuals of both sexes from Oaxaca and from Chiapas probably is due to the small sizes of the samples. The largest female has a snout-vent length of 79.3 mm.; this individual is from the Atlantic slopes of the Mesa Central, Chiapas, México. The largest males are from the Sierra de Juárez

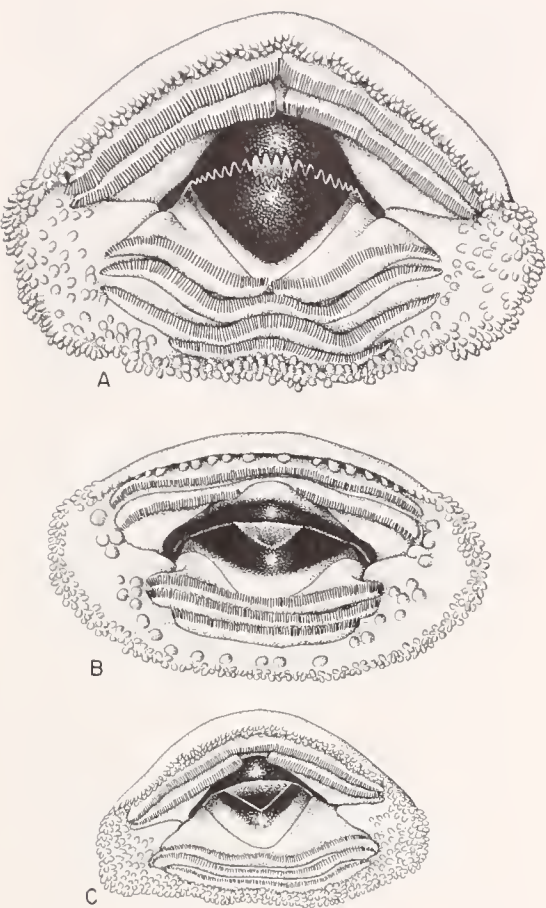


FIG. 229. Mouthparts of tadpoles of species in the *Hyla taeniopus* group. A. *H. chaneque*, K.U. No. 104124. B. *H. taeniopus*, K.U. No. 68498. C. *H. altipotens*, K.U. No. 104182.  $\times 8.5$ .

in Oaxaea, Méxio. The two known specimens from the Pacific slopes of Chiapas are small and possibly are immature.

The head is slightly wider than long and slightly wider than the body; the top of the head is flat or barely convex. The snout is moderately short, truncate in dorsal profile and bluntly rounded in lateral profile. The nostrils are noticeably protuberant and are situated about three-fourths of the distance from the eyes to the tip of the snout. The canthus is angular and distinct; the loreal region is moderately concave, and the lips are thick and barely flared. A moderately heavy supratympanic fold extends posteriorly from the posterior edge of the eyelid above the tympanum and to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posterior to the eye and separated from the eye by a distance slightly greater than the diameter of the tympanum. The eyes are large and protuberant.

The arms are long and moderately slender; there is no axillary membrane. A row of low tubercles forms a dermal fold along the ventrolateral edge of the forearm. A weak transverse dermal fold is present on the wrist. The fingers are long and stout and bear large discs; the width of the disc on the third finger is nearly twice the diameter of the tympanum. The subarticular tubercles are large, round, and flat. The distal tubercle on the fourth finger is barely bifid in some

TABLE 42  
Geographic Variation in Size and Certain Proportions, with Means in Parentheses, in *Hyla chaneque*.

Locality	Sex	N	Snout-vent Length	Tibia Length/ S-V L	Head Length/ S-V L	Tympanum/ Eye
Atlantic slopes, Oaxaca ----	♂	23	52.0-70.9 (57.4)	0.460-0.531 (0.489)	0.313-0.350 (0.332)	0.338-0.560 (0.451)
	♀	5	66.4-74.9 (70.0)	0.473-0.560 (0.509)	0.315-0.347 (0.328)	0.426-0.493 (0.453)
Atlantic slopes, Chiapas --	♂	5	56.0-60.7 (58.9)	0.462-0.511 (0.489)	0.325-0.338 (0.330)	0.418-0.444 (0.429)
	♀	1	79.3	0.481	0.312	0.455
Pacific slopes, Chiapas ----	♂	1	51.5	0.564	0.338	0.485
	♀	1	52.1	0.563	0.361	0.425

specimens; in others it is emarginate. The supernumerary tubercles are moderately large and subconical; they are arranged in a single row or irregularly on the proximal segments of each digit. A double or tripartite outer palmar tubercle is present, but indistinct in many specimens. The prepollex is noticeably enlarged, and in breeding males bear a horny nuptial excrescence. The fingers are no more than one-third webbed (fig. 225A). The webbing is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short but not robust; the heels of the adpressed limbs overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the eye. A transverse, tubercular fold is present on the heel, and a strong tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, elliptical, flat, and broadly visible from above. No distinct outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are large and round; the supernumerary tubercles are moderately large, subconical, and arranged in a single row on the proximal segment of each digit. The toes are about four-fifths webbed (fig. 226A). The webbing extends from the base of the disc of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the middle of the penultimate phalanx of the third, from the base of the disc of the third to the middle of the penultimate phalanx of the fourth, and from the base of the disc of the fourth to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs and is covered by a moderately long, heavy, tubercular anal sheath. Ventrally, the anal opening is bordered by large tubercles. The skin on the head and body is smooth with many small, scattered tubercles; that on the

dorsal surfaces of the legs and ventral surfaces of the shanks is smooth. The throat, chest, belly, and ventral surfaces of the thighs are heavily granular. A thoracic fold is present. The tongue is ovoid or cordiform; in the latter case, it is shallowly notched behind. The prevomerine teeth are on widely separated transverse ridges between the rather small, ovoid choanae. Males have four to nine teeth on each prevomerine process and have a total of nine to 16 (mean, 25 specimens, 12.6); females have six to nine teeth on each process and a total of 12 to 18 (mean, six specimens, 15.2) teeth. In those males having vocal slits, the slits are small and extend for a short distance posterolaterally from the lateral base of the tongue. In these specimens the vocal sac is single, median, subgular, and barely distensible.

The general coloration of *Hyla chaneque* is dull green with darker green blotches and transverse bands on the limbs or brown with darker brown blotches and transverse bands on the limbs (pl. 60, figs. 2 and 3). In life, the holotype (K.U. No. 58439) was dull green above with dark olive-brown spots on the flanks and blotches on the back, and olive-brown transverse bands on the limbs. The flanks were creamy green, and the posterior surfaces of the thighs were dark brown. The ventral surfaces were dull creamy brown, and the throat was spotted with darker brown. In some individuals the dorsal blotches are very dark brown, nearly black. The blotches are irregular in shape, but in many individuals are present as two large longitudinal spots beginning on the eyelids or in the occipital region and extending to the sacral region. In some of these specimens, the large spots are fragmented into two or more spots on each side. Furthermore, spots of various sizes are present between the longitudinal blotches; some of these spots are fused with the longitudinal blotches. The spots on the flanks are round and discrete. The supratympanic fold is dark brown. The dark transverse bands on the hind limb are wider than the pale interspaces; usually three or four bands are present on each thigh and shank. Transverse bands are present on the foot and the fourth and fifth toes. The posterior surfaces of the



thighs are creamy brown, dark brown, or black with faint bluish white flecks. The ventral coloration varies from a creamy tan or dark brown. In those specimens having a pale venter, dark brown spots are present on the throat in some individuals. Likewise, in those having a brown venter, brown spots are barely visible in some individuals. In many specimens having a brown venter, small, distinct, white flecks are present, especially on the chest and ventral surfaces of the shanks. The iris is bronze to a pale copper-color with dark brown or black reticulations.

In preservative, the dorsum is tan or gray with brown or black markings. Then venter is creamy tan to dark brown; the white flecks persist on the venter, and in those specimens having bluish white flecks on the thighs in life, the flecks are white in preservative.

The highly variable coloration in this species does not seem to show any geographic trends. Specimens with pale and dark ventral coloration are known from Chiapas and Oaxaca. In the specimens available from Chiapas all have dark brown posterior surfaces of the thighs and lack bluish-white flecks on the thighs. Most specimens from Oaxaca have extremely dark brown or black posterior surfaces of the thighs with small bluish-white flecks present. There is no noticeable color change from night to day in this species.

**TADPOLES:** Various developmental stages are available for study. The smallest tadpoles are in developmental stage 25 and have a body length of 9.4 mm. and a total length of 28.0 mm. The largest tadpoles are in developmental stage 42 and have body lengths of 20.0 to 23.0 mm. (table 43). A typical tadpole in developmental stage 27 from 4.2 kilometers south of Campamento Vista Hermosa, Oaxaca, México, has a total length of 53.0 mm. and a body length of 19.0 mm. The body is relatively small, whereas the tail is long and muscular. The body is slightly depressed, but only barely wider than deep. The top of the head is flat; in dorsal profile the snout is bluntly rounded, and in lateral profile, it is acutely rounded. The nostrils are protuberant, directed anterolaterally and sit-

uated about midway between the eye and the tip of the snout. The eyes are small, about one-sixth of the depth of the body; they are dorsolateral and directed dorsolaterally. The spiracle is sinistral; its opening is directed posterodorsally at a point near the middle of the body. The anal tube is long and dextral. The lateral line organs form a row from the snout posteriorly, median to the nostril and eye and thence laterally to a point posteroventral to the eye. The organs form a second row beginning at the same place on the snout; this row passes laterally to the nostril and ventral to the eye to meet the first row. At a point below the eye another row of organs extends ventrally across the belly. At the point of junction of the two rows behind the eye, one row continues posteriorly onto the midlateral surfaces of the tail and thus continues on the tail to the tip of the musculature; a second row diverges from the point behind the eye and extends posteroventrally to a point just beyond the spiracular opening where the row turn ventral and continues across the belly. The caudal musculature is heavy and extends nearly to the base of the tail. The fins are relatively shallow; at midlength of the tail the musculature is deeper than either fin. Terminally the caudal fins are rounded; the dorsal fin does not extend onto the body (fig. 228A).

The top of the head is dark brown; the sides of the head and body are yellowish tan, and the belly is dark gray. The caudal musculature is pale brown. The dark brown spots are scattered on the caudal musculature and fins. The xanthophores form distinct yellow spots on the caudal musculature and fins and a distinct yellow edge on the dorsal fin; the iridophores form pale green streaks on the body. The iris is pale yellow.

In preservative, the dorsal and lateral surfaces of the body are pale brown or olive-brown, darkest ventrally. The caudal musculature is yellowish tan; the caudal fin is translucent with numerous small brown spots.

The mouth is anteroventral, directed ventrally, and not as wide as the body. A shallow lateral fold is present. The mouth is completely fringed by two or three rows of small papillae; additional scattered papillae

TABLE 43  
 Sizes and Proportions of Tadpoles, with Means in Parentheses, in Relation  
 to Developmental Stages, of *Hyla chaneque*.

Stage	N	Body Length	Tail Length	Total Length	Body/Tail
25	16	9.4-17.2 (14.2)	15.7-37.1 (29.0)	28.0-61.0 (43.8)	0.413-0.796 (0.516)
27	6	19.0-22.5 (20.0)	34.0-50.5 (41.4)	53.0-73.0 (61.4)	0.445-0.558 (0.490)
28	2	19.0	36.0-37.0 (36.5)	55.0-56.0 (55.5)	0.513-0.527 (0.520)
29	5	19.0-20.0 (19.6)	35.0-40.5 (39.4)	54.0-60.5 (59.0)	0.481-0.542 (0.498)
30	3	19.0-21.0 (20.0)	35.0-40.0 (37.0)	55.0-61.0 (57.0)	0.525-0.571 (0.541)
31	2	19.0-21.0 (20.0)	39.0-40.0 (39.5)	59.0-60.0 (59.5)	0.475-0.538 (0.506)
32	1	20.0	39.0	59.0	0.512
33	1	23.0	40.0	63.0	0.575
34	1	21.0	39.0	60.0	0.538
35	1	21.0	41.8	62.8	0.502
37	2	22.0-23.0 (22.5)	38.0-40.0 (39.0)	61.0-62.0 (61.5)	0.575-0.605 (0.590)
38	3	18.0-19.8 (19.1)	35.0-42.2 (38.2)	53.0-62.0 (57.3)	0.469-0.520 (0.501)
39	1	20.5	41.0	61.5	0.500
42	4	20.0-23.0 (21.8)	19.3-29.0 (25.0)	40.3-50.0 (46.8)	0.689-1.088 (0.887)

are present laterally. Both beaks are massive and bear large, pointed serrations. The upper beak forms a high arch with small slender lateral processes; the ventral beak is robust and V-shaped. There are two upper and four lower rows of teeth. The upper rows are equal in length and extend to the papillae; the second upper row is narrowly interrupted medially. The first three lower rows are equal in length but noticeably shorter than the upper rows. The fourth lower row is much shorter than the other lower rows (fig. 229A).

**MATING CALL:** The call of *Hyla chaneque* consists of a single, low-pitched note. The note repetition rate usually is 15 seconds to a minute or more, but one individual produced two notes in quick succession followed by the usual interval and then two more notes (17-2-66-5-30-2 seconds). Each note has a duration of 0.47 to 0.75 (mean, five recordings, 0.59) of a second and a rate of 49 to 70 (mean, 59) pulses per second. The energy

is concentrated in a span from about 800 to 2500 cycles per second, and the dominant frequency is 1500 to 1863 (mean, 1674) cycles per second (pl. 18, fig. 3).

**NATURAL HISTORY:** *Hyla chaneque* inhabits cloud forests. In this moist environment, the frogs apparently are active throughout the year. They have been found at night along the streams in the cloud forests on the northern slopes of the Sierra de Juárez, in the months of January through August. Males are seldom heard to call, but three calling males were found near Campamento Vista Hermosa, Oaxaca, in June, 1964, and two males were heard at the same locality in February, 1966. Another male was calling from a darkened crevice behind a waterfall by day. These frogs are always found in the proximity of cascading mountain streams. At night males and females alike sit on branches of small trees over the streams.

The tadpoles live in pools in the moun-



tain streams. They lie on the bottom of the pool, and when disturbed they seek refuge between small rocks or under larger ones.

REMARKS: In the original description of *Hyla chaneque* Duellman (1961a, p. 4) mentioned the presence of brown spots on the throat in this species. Duellman (1965b, p. 165) restated the coloration of *Hyla chaneque*. Lynch and Smith (1966, p. 60) obtained two specimens of a tree frog from the Sierra Madre north of Zanatepec, Oaxaca, México. One of these specimens had bold brown spots on the throat and anterior part of the chest. The other had faint spots along the edge of the chin. Lynch and Smith selected the heavily spotted specimen as the holotype of a new species, *Hyla duellmani*. Comparison of these two specimens with six individuals from the northern slopes of the Mesa Central in Chiapas and a series of specimens from the Sierra de Juárez in northern Oaxaca reveals that *Hyla duellmani* is not a valid species. The holotype of *duellmani* (U.I.M.N.H. No. 56821) is more heavily spotted on the chin than any other specimen of *chaneque* examined. However, the spotted condition is approached by one specimen from northern Chiapas and by six from northern Oaxaca. In their description of *Hyla duellmani*, Lynch and Smith (1966, pp. 60-62) presented no other characters that will distinguish *duellmani* from *chaneque*. Further examination of the specimens of *duellmani* reveal no characters that will serve to distinguish *duellmani* from *chaneque*. The holotype of *Hyla duellmani* represents an extreme condition of gular spotting, not a distinct species.

All males from the Sierra de Juárez, Oaxaca, have vocal slits. Poorly defined slits are present in one male from Chiapas; in the other five males (including the type of *Hyla duellmani*), a weak groove is present in the floor of the mouth, but there is no opening into a vocal pouch.

ETYMOLOGY: The specific name is derived from a mythological creature in Indian folklore in southern México; this leprechaun-like creature, the chaneque, lives behind waterfalls by day and ventures forth only by night.

DISTRIBUTION: *Hyla chaneque* inhabits

cloud forests from elevations of 800 to 2200 meters on the northern slopes of the Sierra de Juárez in northern Oaxaca, elevations between 1600 and 1700 meters on the Atlantic slopes of the Mesa Central in Chiapas, and elevations of about 1500 meters in the Sierra Madre in extreme eastern Oaxaca, México (fig. 230).

See Appendix 1 for the locality records of the 65 specimens examined.

### *Hyla taeniopus* Günther

*Hyla taeniopus* Günther, 1901 (1885-1902), p. 269 [syntypes, B.M.N.H. Nos. 1947.2.23.32 and 1947.2.23-33 from Jalapa, Veracruz, México; Mateo Trujillo collector]. Kellogg, 1932, p. 175. Smith and Taylor, 1948, p. 89. Duellman, 1965b, p. 159.

*Hyla bromeliana* Taylor, 1939c, p. 97 [holotype, F.M.N.H. No. 100075 (formerly E.H.T.-H.M.S. No. 16630) from near Tianguistengo, Hidalgo, México; Hazel Roberts and Edward H. Taylor collectors]. Smith and Taylor, 1948, p. 90.

*Hyla proboscidea* Taylor, 1948a, p. 259 [holotype, K.U. No. 23626 from 2 kilometers west of Jico (Xico), Veracruz, México; Walter W. Dalquest collector (not *Hyla proboscidea* Brongersma, 1933, from Gran Río, Surinam)].

*Hyla dalquesti* Taylor, 1949a, p. 74 [replacement name for *Hyla proboscidea* Taylor, 1948a, preoccupied].

*Hyla cyclomaculata* Taylor, 1949c, p. 272 [holotype, K.U. No. 26954 from Huatusco, Veracruz, México; Walter W. Dalquest collector].

DIAGNOSIS: This is a large tree frog (males attain a snout-vent length of 66 mm. and females, 70 mm.) having a green or brown dorsum with darker green or brown blotches on the body and transverse bands on the limbs. The venter varies from immaculate creamy white to dusty brown with or without dark brown spots. *Hyla taeniopus* differs from other members of the *Hyla taeniopus* group by having an acuminate, protruding snout in males and a truncate snout in females. Furthermore, *taeniopus* differs from *chaneque* by having the skin on the dorsum smooth, instead of tuberculate and by having a larger tympanum. *Hyla altipotens* differs from *taeniopus* by having an acuminate snout in both sexes and by having longer legs and a smaller head (see table 41). The only other frogs in northern Middle America that might be confused with *taeniopus* are *Smilisca baudinii* and *cyanosticta*. Both have

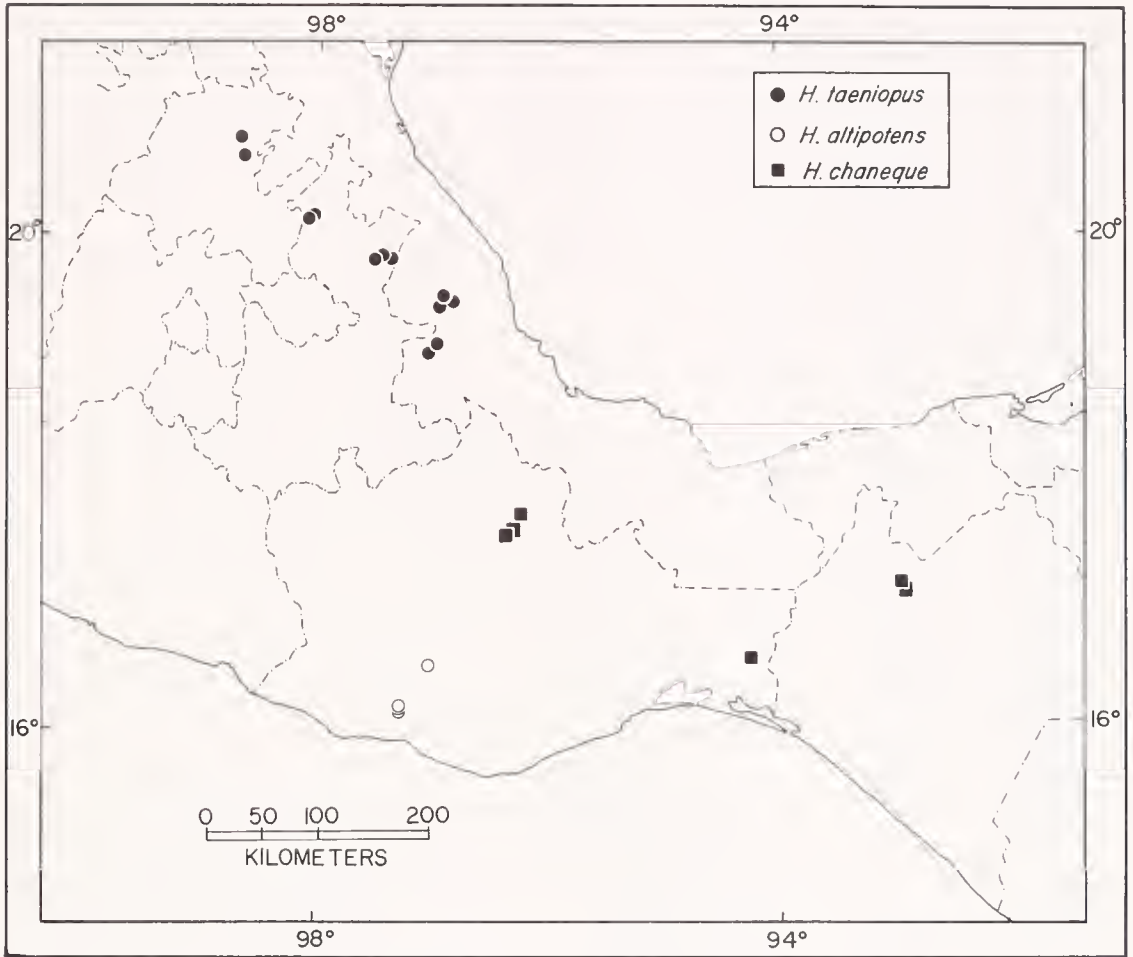


FIG. 230. Distribution of the species in the *Hyla taeniopus* group.

immaculate creamy white or creamy yellow venters and a dark postorbital mark; *baudinii* has a blunt snout in both sexes, whereas *cyanosticta* has an acuminate, but not protruding snout in both sexes, and blue spots on the flanks and posterior surfaces of the thighs.

**DESCRIPTION:** This is a moderately large frog; males attain a maximum snout-vent length of 65.9 mm., and females reach 70.0 mm. In a sample of 18 adult males from throughout the range in eastern México, the snout-vent length is 48.0 to 65.9 (mean, 58.0) mm.; the ratio of tibia length to snout-vent length is 0.450 to 0.500 (mean, 0.480); the ratio of head length to snout-vent length is 0.290 to 0.340 (mean, 0.310); the ratio of head width to snout-vent length is 0.260 to

0.300 (mean, 0.280), and the ratio of the diameter of the tympanum to that of the eye is 0.510 to 0.620 (mean, 0.560). In eight females from the same area, the snout-vent length is 56.6 to 70.0 (mean, 64.2) mm. In most proportions, the females do not differ from the males, but females do have a slightly larger tympanum in relation to the diameter of the eye; the tympanum/eye ratio in females is 0.540 to 0.660 (mean, 0.620).

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is acuminate in males and truncate in females. In lateral profile, the snout gradually slopes downward anterior to the nostrils and protrudes beyond the lower jaw in males; it is rounded and barely protruding in fe-

males (fig. 231). The snout is moderately long in both sexes, and the nostrils are situated at a point about two-thirds the distance from the eyes to the tip of the snout. The nostrils are noticeably protuberant. The canthus is angular; the loreal region is noticeably concave, and the lips are thick and barely flared. A heavy dermal fold extends posteriorly from the posterior edge of the eye, above the tympanum, and downward to a point above the insertion of the arm. In all specimens, this dermal fold covers the upper edge of the tympanum; in some others it also obscures the posterior edge. Otherwise, the tympanum is distinct and is separated from the eye by a distance equal to the diameter of the tympanum. The eyes are large and protuberant.

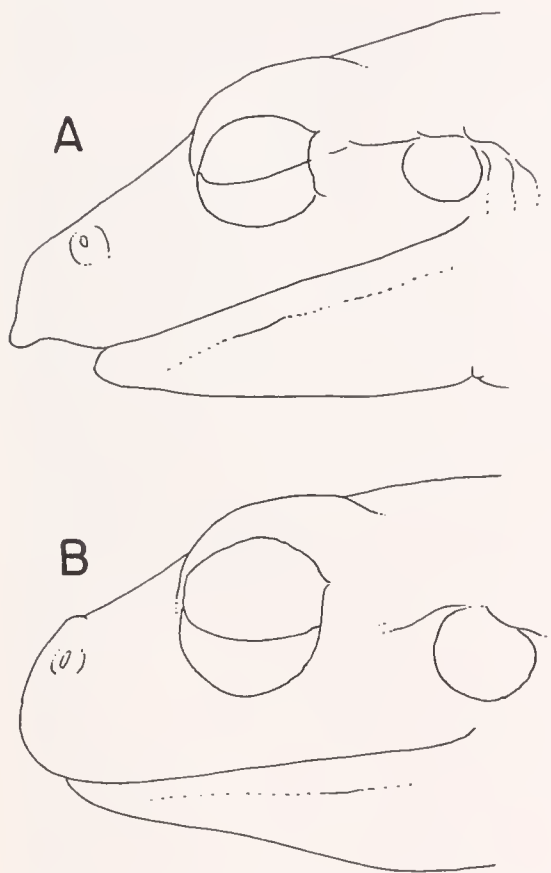


FIG. 231. Sexual dimorphism in the shape of the snout in *Hyla taeniopus*. A. Male, K.U. No. 53825. B. Female, K.U. No. 53833.  $\times 8$ .

The arms are long and moderately slender. There is no axillary membrane. A row of tubercles forms a dermal fold along the ventrolateral edge of the forearm; in most specimens this fold continues onto the fourth finger. A distinct transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear large discs. The disc on the third finger is about half again the size of the tympanum. The subarticular tubercles are large and round; the supernumerary tubercles are small and subconical. The outer palmar tubercle is tripartite. An elongate tubercle is present on the base of the pollex. The pollex is greatly enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-third webbed (fig. 225B). The webbing is vestigial between the first and second fingers and extends from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third and on to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A transverse dermal fold is present on the heel, and a strong tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, flat, elliptical, and broadly visible from above. The outer metatarsal tubercle, if present, is indistinct. The toes are long and slender, and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are large and conical. The supernumerary tubercles are small and conical. The toes are about three-fourths webbed (fig. 226B). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and onto the base of the disc of the fifth toe.

The anal opening is directed ventrally at the level of the ventral surfaces of the thighs. The anal tube is long and tuberculate. The



skin on the dorsum, anterior and posterior surfaces of the thighs, and ventral surfaces of the shanks and tarsi is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. The tongue is ovoid, emarginate or barely notched posteriorly, and free behind for about one-fourth of its length. The denticulous processes of the prevomers form transverse ridges between the small round choanae. Four to eight teeth are present on each prevomerine process. The total number of prevomerine teeth is nine to 16 (mean, 12.7 in males, and 13.3 in females). The vocal slits are small and are situated posterolaterally near the angles of the jaws. The vocal sac is single, median, subgular, and barely distensible.

The general coloration of *Hyla taeniopus* is green or brown with darker green or brown blotches on the body and transverse bands on the limbs (pl. 61, figs. 1 and 2). The brown dorsal coloration is more common in females than in males, but even the darkest brown females are capable of changing to pale greenish tan with olive-green markings. Typical coloration of an adult female consists of a reddish brown dorsum with irregular darker brown markings middorsally. The flanks are dark brown with lemon yellow spots narrowly bordered by black. The belly is brownish black with yellow flecks, and the throat is silvery white. The typical coloration of an adult male is greenish tan above with darker olive-green blotches and brown flecks. The flanks are pale greenish yellow with dark brown spots. The posterior surfaces of the thighs are dark brown; the ventral surfaces of the limbs, anterior surfaces of the thighs, and webbing of the feet are pale gray. The belly and throat are dusty white with gray spots. The iris is bronze or grayish bronze in adults of both sexes. Usually males have pale greenish yellow or yellow flanks with dark green, brown, or black mottling; females usually have dark green, dark brown, or sometimes black flanks with yellow spots. All individuals have dark dorsal markings on the body and dark transverse bands on the limbs and feet. Usually there are three or four transverse bands on the shank and thigh, and four and five bands on the feet.

A north-south trend in variation in color-

ation is apparent. Comparisons are made below between three series: 1) Vicinity of Tlanguistengo, Hidalgo, 2) Río Octapa, near Tezuatlán, Puebla, and 3) Central Veracruz. In general, there is a tendency toward a darker venter, especially in females, from north to south. All females and most males from Hidalgo have immaculate creamy white venters; some males have scattered brown or black spots on the chest and flanks. Some males from the Río Octapa are immaculate below, but most individuals have some spotting on the flanks, chin, and chest; others have brown throats and brown laterally on the belly. Some females are immaculate below, but most have darkened venters and brown flanks. Some males from Veracruz have pale venters with scattered dark spots, but most have a dusty brown venters with darker brown flanks, where there is a distinct yellow spotting or marbling. Females have a darker brown venter, often with distinctive darker flanks with yellow spots.

Ontogenetic changes in coloration also are apparent. A recently metamorphosed individual (K.U. No. 65062) with a snout-vent length of 23.6 mm. had a bright green dorsum with small black flecks on the head and body in life. The flanks were pale green and the venter was immaculate pale yellow. The limb bands were dark brown, and the iris was metallic green. With increased size, there is a gradual change in dorsal coloration from many small black flecks to fewer large spots, which in many specimens are fused to form irregular blotches. Increased melanophore development on the flanks, especially in females, results in dark mottling or spotting on yellowish flanks; in large females, the flanks may be dark brown or black with yellow spots. Increased melanophore development also occurs on the belly. Juveniles having snout-vent lengths of about 30 mm. have a few large black spots on the throat and chest. Individuals having snout-vent lengths of about 45 mm. have large round, dark spots on the venter or an overall general darkening of the ventral surfaces. All individuals having snout-vent lengths less than 36 mm., in addition to a few larger specimens, have a metallic green iris in life. Subadults (37 to 50 mm.) have a pale bronze iris, sometimes with a

silvery or greenish tint. In adults, the iris is bronze, often with a noticeably darker, sometimes copper-colored, periphery.

Although no noticeable geographic variation in size or structural features is apparent, there is an ontogenetic change in the shape of the snout in males. The snout is truncate in juveniles, but in young males, having snout-vent lengths of about 40 mm., a slight protrusion of the snout is noticeable. The sloping, protruding snout, characteristic of the adult males, is developed by the time the frogs reach a length of 50 mm. Furthermore, in juveniles, the webbing on the hand is barely evident, and the feet are only about one-half webbed. The amount of webbing increases with age to the condition previously described for the adults.

**TADPOLES:** Four tadpoles of this species are available for study. The smallest specimen (developmental stage 25) has a body length of 13.6 mm. and a total length of 31.1 mm. The most advanced tadpole (developmental stage 30) has a body length of 18.5 mm. and a total length of 51.2 mm. A typical tadpole in developmental stage 25 has a body length of 16.5 mm. and a total length of 46.2 mm. The body is moderately depressed, slightly wider than deep. In dorsal profile the snout is bluntly rounded, and in lateral profile acutely rounded. The eyes are small and directed dorsolaterally; the diameter of the eye is equal to about one-sixth the depth of the body. The nostrils are small, directed anterolaterally, and situated about midway between the eyes and the tip of the snout. The spiracle is sinistral; the spiracular opening is directed posterodorsally at about midlength of the body. The anal tube is dextral and long. The caudal musculature is heavy and extends nearly to the tip of the tail. At midlength of the tail, the depth of the musculature is much greater than the depth of either the dorsal or ventral fins. The dorsal fin does not extend onto the body; distally, the fins are rounded (fig. 228B).

The body is brownish black and the caudal musculature is slightly paler. Melanophores form dense brownish black spots on the tail, and xanthophores form a distinct orange-yellow edge to the dorsal fin. Iridophores form silvery green flecks on the body.

The iris is pale bronze. In preservative the body is dark grayish brown, darker ventrally. The caudal musculature is grayish tan; the caudal fin is translucent. Numerous dark brown spots are present on the caudal musculature and fin.

The mouth is small, located anteroventrally, and directed ventrally. The lips have a shallow lateral fold. Two rows of small papillae completely border the mouth; medial to these is a row of larger papillae. The upper beak forms a broad arch with robust lateral processes. The lower beak is massive and broadly V-shaped. Both beaks bear fine serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length, and the second upper row is broadly interrupted medially. The lower rows are complete, shorter than the upper rows, and the third lower row is the shortest (fig. 229B).

**MATING CALL:** *Hyla taeniopus* has not been heard to call in the field; recordings of the call are not available. One individual kept in captivity uttered one loud groan-like note. On the basis of this one observation and the presence of vocal slits, it may be assumed that this species does possess a voice. However, the significance of voice in the mating behavior is quite questionable.

**NATURAL HISTORY:** *Hyla taeniopus* inhabits cloud forests characterized by moderately low temperatures and high humidity. Individuals have been found on vegetation along cascading mountain streams at night and on elephant ear plants, lilies, and arboreal bromeliads by day. Breeding apparently takes place in the dry season, when the streams are clear and relatively quiet. Adults in breeding condition have been found in December, January, and February.

Tadpoles were obtained from a gravel-bottomed pool in a rocky stream in a cloud forest.

As pointed out by Duellman (1965b, p. 164) breeding males of *Hyla taeniopus* have greatly enlarged testes. In the breeding season, the testes essentially fill the body cavity, much in the same way eggs do in a gravid female. Breeding apparently takes place in streams having a steep gradient. The rapidly flowing water would have a tendency to wash

away the sperm as they were being emitted over the eggs. Consequently, the development of large testes capable of producing great quantities of sperm possibly is an adaptation to insure fertilization.

REMARKS: Duellman (1965b) discussed the taxonomic status of the names *Hyla taeniopus*, *Hyla bromeliana*, *Hyla dalquesti*, and *Hyla cyclomaculata*. The striking differences between adults of each sex and juveniles of *Hyla taeniopus* has resulted in the application of four specific names to this species. The syntype of *Hyla taeniopus* examined by me (B.M.N.H. No. 1947.2.23.32) is a juvenile having a snout-vent length of 30.3 mm.; the holotype of *Hyla bromeliana* (F.M.N.H. No. 100075) likewise is a juvenile having a snout-vent length of 26.9 mm. Taylor (1948a) named *Hyla proboscidea* [= *Hyla dalquesti* (Taylor, 1949a)] on the basis of five adult males from Jico, Veracruz, and Taylor (1949c) named *Hyla cyclomaculata* on the basis of a single female from Huatusco, Veracruz, México. As demonstrated by Duellman (1965b) the acquisition of a series of these frogs has provided the necessary material to demonstrate that only a single species is involved.

ETYMOLOGY: The trivial name *taeniopus*, is derived from the Latin *taenia*, meaning band and the Latin *pes*, meaning foot. The name alludes to the transverse bands on the limbs.

DISTRIBUTION: *Hyla taeniopus* occurs at elevations between 1200 and 2100 meters on the Atlantic slopes of the Sierra Madre Oriental from northeastern Hidalgo, southward through eastern Puebla to central Veracruz, México (fig. 230).

See Appendix 1 for the locality records of the 72 specimens examined.

### *Hyla altipotens* Duellman

*Hyla altipotens* Duellman, 1968a, p. 572 [holotype, K.U. No. 101001 from 37 kilometers north (by road) of San Gabriel Mixtepec, Oaxaca, México, elevation 1860 meters; William E. Duellman collector].

DIAGNOSIS: This is a large frog (adults of both sexes attain snout-vent lengths of 75 mm.) having a green or tan dorsum with darker green or brown spots on the body and transverse bands on the limbs and with or

without a middorsal dark line. The head is narrow, and the snout is acuminate in both sexes. The skin is smooth on the dorsum. The venter is immaculate yellow, and a bronze-colored canthal stripe is present. *Hyla taeniopus* differs from *altipotens* by having a blunt snout in females, larger head, and shorter legs (see table 41). Furthermore, the venter in *taeniopus* is creamy white to brown, not yellow, and *taeniopus* lacks a canthal stripe. *Hyla chaneque* differs from *altipotens* by having a blunt snout in both sexes, a tuberculate dorsum, and in proportions (see table 41). Juveniles of *altipotens* can be confused with *Hyla pinorum*, some individuals of which have a dark middorsal line. Otherwise, *pinorum* differs from *altipotens* by having a smaller tympanum, less webbing on the hands, and a short, truncate snout.

DESCRIPTION: The maximum known snout-vent length in both males and females of this large species is about 75 mm. In a sample of five adult males from the type locality, the snout-vent length is 68.8 to 75.1 (mean, 70.7) mm.; the ratio of tibia length to snout-vent length is 0.526 to 0.558 (mean, 0.537); the ratio of foot length to snout-vent length is 0.452 to 0.481 (mean, 0.472); the ratio of head length to snout-vent length is 0.281 to 0.300 (mean, 0.292); the ratio of head width to snout-vent length is 0.303 to 0.313 (mean, 0.308), and the ratio of the diameter of the tympanum to that of the eye is 0.414 to 0.552 (mean, 0.506). Two adult females from the type locality have snout-vent lengths of 69.4 and 75.3 (mean, 72.4) mm. The females differ from the males by having slightly longer legs and larger tympani; the ratio of tibia length to snout-vent length in the two females is 0.558 and 0.562 (mean, 0.560), and the ratio of the diameter of the tympanum to that of the eye is 0.533 to 0.630 (mean, 0.588). Most known specimens of this species are immature; 19 individuals have snout-vent lengths of 31.6 to 50.1 mm. There are no significant differences in proportions in these small specimens from the adults.

The head is relatively small; it is not as wide as the body. The top of the head is flat or barely convex. The snout in dorsal profile is acuminate; in lateral profile the snout is acutely rounded and protruding be-



yond the tip of the lower jaw. The snout is moderately long; the nostrils are slightly protuberant, directed dorsolaterally, and situated about two-thirds of the distance from the eyes to the tip of the snout. The canthus is angular, and the loreal region is flat; the lips are thick barely flared. A heavy dermal fold extends posteriorly from the posterior corner of the eye over the dorsal edge of the tympanum and curves ventrally to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long and robust. An abbreviated axillary membrane is present. A thin dermal fold is present on the ventrolateral edge of the forearm, and a distinct, transverse dermal fold is present on the wrist. The fingers are moderately short and broad and bear large discs; the width of the disc on the third finger is greater than the diameter of the tympanum. The subarticular tubercles are large, round, and conical; none is bifid. The supernumerary tubercles are large and granule-like; they are present only on the proximal segments of the digits. The prepollex is enlarged, but breeding males apparently do not develop nuptial excrescences. The fingers are about one-half webbed (fig. 225C). The webbing connects the first and second fingers at the level of the distal end of the antepenultimate phalanx, extends from the middle of the penultimate phalanx of the second finger to the middle of the antepenultimate phalanx of the third, and between the bases of the penultimate phalanges of the third and fourth fingers. The hind limbs are long and slender; the heels of the adpressed limbs overlap by about one-half of the length of the shank. The tibiotarsal articulation extends to a point between the eye and the nostril. A thin, transverse dermal fold is present on the heel; the tarsal fold is strong and extends the full length of the tarsus. The inner metatarsal tubercle is relatively small, elongate, and barely visible from above. The outer metatarsal tubercle is small and conical. The toes are moderately long and slender; the discs are slightly smaller than those on the

fingers. The subarticular tubercles are large, round, and subconical. The supernumerary tubercles are large, conical, and arranged in a single row on the proximal segment of each digit. The toes are about four-fifths webbed (fig. 226C). The webbing extends from the base of the disc of the first to the base of the disc of the second and onto the base of the penultimate phalanx of the third toe, from the base of the disc on the third to the base of the penultimate phalanx of the fourth and onto the base of the disc of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thigh; the anal sheath is long and tubular. The skin is smooth on the dorsal surfaces of the body and limbs and on the ventral surfaces of the shanks; it is granular on the throat, belly, and ventral surfaces of the arms and thighs. The tongue is ovoid, widest posteriorly, and neither notched nor noticeably free behind. The dentigerous processes of the prevomers are robust transverse ridges between the small, ovoid choanae. The number of prevomerine teeth on each process varies from five to 10; the total number of prevomerine teeth is 10 or 12 (mean, two specimens, 11.0) in females, and 13 to 18 (mean, five specimens, 15.0) in males. The vocal slits and a vocal sac are absent.

The general coloration of *Hyla altipotens* is tan or pale green above with darker brown or green spots on the back and transverse bands on the limbs (pl. 60, fig. 1 and pl. 61, fig. 3). The typical coloration of an adult male is pale green above with slightly darker green spots. The dorsal surfaces of the upper arms and thighs are tan with green transverse bars. The upper surfaces of the forearms and shanks are green with darker green transverse bars. The feet, fourth and fifth toes, and third and fourth fingers are tan with brown transverse bars; the other fingers and toes are tan with brown flecks. The ventral surfaces are creamy yellow, brightest on the throat and chest. The flanks and anterior surfaces of the thighs are bright creamy yellow with dark brown reticulations and spots. The posterior surfaces of the thighs and ventral surfaces of the hand and webbing on the hands and feet are yellowish tan. There is a narrow, tan labial stripe. Narrow, cream-



colored stripes are present on the ventrolateral edge of the forearms, along the outer edge of the foot, and above the anus. A bronze-colored stripe extends the length of the canthus, along the edge of the upper eyelid, and onto the supratympanic fold. The iris is pale bronze with black reticulations and a faint, median, horizontal copper-colored streak. The pupil is horizontally elliptical with a ventral notch. The palpebral membrane is clear above and pale bluish green with faint brown reticulations below.

In preservative, the dorsum is pale brown with many darker brown spots on the back and dark brown transverse bands on the limbs. The flanks are white with dark brown spots; the anterior surfaces of the thighs are creamy white with brown reticulations and the posterior surfaces of the thighs are dark brown with creamy yellow flecks. The stripe on the snout, canthus, edge of upper eyelid, and supratympanic fold is tan; the ventral surfaces of the feet are brown, and the rest of the venter is creamy white.

All individuals have creamy yellow venters and yellow flanks and anterior surfaces of thighs with brown or black spots and mottling. Most of the adults were pale green with darker green spots, but one individual was a much darker olive-green, and one was uniform brown above with a dark brown mid-dorsal stripe. Most subadults (snout-vent lengths, 31.6 to 50.1 mm.) were pale reddish tan above with darker reddish brown bars on the limbs and blotches on the back. The side of the head is dark brown and the stripe along the canthus, edge of upper eyelid, and the supratympanic fold is yellowish tan. Some individuals had a dark brown middorsal stripe. The posterior surfaces of the thighs were a dull yellowish tan; yellow flecks were present in the larger individuals. The number of transverse bands on each thigh and shank varies from five to eight. The white stripe above the anus and the stripe from the snout along the side of the head are invariably present. In some of the largest individuals, the brown reticulations on the anterior surfaces of the thighs extend onto the ventral surfaces; in these specimens, brown flecks are present on the ventral surfaces of the shanks.

**TADPOLES:** A typical tadpole in develop-

mental stage 25 from 13 kilometers north-northeast of Juchatengo, Oaxaca, México, has a body length of 13.8 mm. and a total length of 41.1 mm. The body is slightly depressed and noticeably wider than deep. In dorsal profile, the snout is bluntly rounded; in lateral profile, it slopes gently from the eyes to a point above the nostrils and is further inclined to an abbreviated, truncate snout. The eyes are small and directed dorsolaterally. The nostrils are slightly protuberant and are situated about midway between the eyes and the tip of the snout. The spiracle is sinistral; the spiracular opening is directed posterodorsally at a point below the midline and about two-thirds the distance of the length of the body. The anal tube is moderately long and dextral. The caudal musculature is moderately robust. The tail is long; the caudal fins are low. At midlength of the tail the depth of the caudal musculature is greater than the depth of either the dorsal or ventral fins. The dorsal fin barely extends onto the body. Terminally, the fins are rounded (fig. 228C).

The body is dark brown or black; minute golden flecks are present on the sides and belly. The caudal musculature is brown laterally and ventrally and dark brown, nearly black dorsally. Faint brown flecks are present on the fins. In preservative the coloration is much like that in life, except that the gold flecks have disappeared and that the caudal musculature is creamy tan, dark brown dorsally. In life, the iris is pale gold.

The mouth is small and ventral. A moderately deep lateral fold is present in the lips. The mouth is completely bordered by two or three rows of small papillae; additional papillae are present in the lateral fold. The upper beak is robust and in the form of a broad arch with long slender lateral processes. The lower beak is broadly V-shaped. Both beaks bear moderately long, blunt serrations. There are two and three lower rows of teeth. The upper rows are equal in length and extend nearly to the edges of the lips; the second upper tooth row is broadly interrupted medially. The lower rows are complete, approximately equal in length, and all slightly shorter than the upper rows (fig. 229C).

**MATING CALL:** The absence of vocal slits

and apparent absence of a vocal sac strongly suggest that this species lacks a voice.

**NATURAL HISTORY:** This is a stream-breeding species that inhabits cloud forests and pine-oak forests. All known specimens were found in the dry season. At that time, adults and juveniles alike were found in trees and bushes near streams. Tadpoles were obtained from quiet pools in rocky streams.

*Hyla altipotens* is like *Hyla taeniopus* in having greatly enlarged testes. If the large size of the testes is correlative with increased production of sperm, the large size of the testes may be an adaptation for successful breeding in torrential streams (fig. 232).

Two tadpoles were raised to metamorphosis. The tadpoles were obtained in developmental stage 25 on February 19, 1966; they metamorphosed on March 26, 1966. The young had snout-vent lengths of 17.5 and 19.7 mm. The dorsum was dark green (capable of changing to dark brown). A dark brown

stripe extended from the nostril to a point above the insertion of the arm. The eanthal stripe was pale greenish bronze. The anterior and posterior surfaces of the thighs, ventral surfaces of the limbs, and hands were dark yellow. The chin and belly were pale yellow. The iris was bronze medially and a coppery color peripherally.

**REMARKS:** Duellman (1965b, p. 166) listed a specimen (T.C.W.C. No. 16184) of supposed *Hyla chaneque* from Los Fustes, 3 kilometers east of San Sebastian, Oaxaca, México. Re-examination of this specimen reveals that it is *Hyla altipotens*.

**ETYMOLOGY:** The specific name *altipotens* is Latin, meaning mighty, used in allusion to the supposed potentiality of fertilization by the production of vast quantities of sperm in large testes.

**DISTRIBUTION:** *Hyla altipotens* occurs on the Pacific slopes of the Sierra Madre del Sur in Oaxaca, México, where it lives in cloud forests and pine-oak forests at elevations between 1100 and 1900 meters (fig. 230).

See Appendix 1 for the locality records of the 31 specimens examined.

#### The *Hyla bistincta* Group

**DEFINITION:** The members of this group are medium-sized, stream-breeding species; males attain a maximum snout-vent length of 54 mm. and females, 56 mm. No marked sexual dimorphism in size is evident. Frogs in this group are rather drab in appearance. The dorsum is dull green, gray, yellow, or various shades of brown. The most distinctive aspect of coloration is the different color patterns on the flanks and posterior surfaces of the thighs. The flanks in all species are spotted or reticulated. The palpebral membrane is clear. The fingers are long and have little webbing (figs. 233 and 234), and the toes are at least two-thirds webbed (figs. 234 and 235). A broad, flat, ossified prepollex is present but does not project as a spine. The skin of the dorsum is thick and glandular, but not tuberculate, in all but *charadricola* and *chryses*, in which it is thin. Dermal fringes and appendages are lacking on the limbs; an axillary membrane is present in *charadricola*, and *chryses*, and a thoracic fold is present in

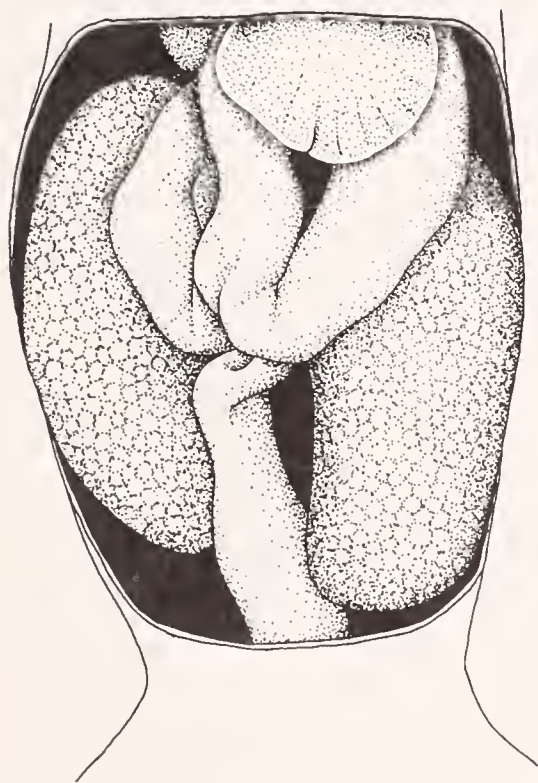


FIG. 232. Ventral view of the viscera of a male *Hyla altipotens* (K.U. No. 101008) showing the large granular testes.  $\times 5$ .

*pachyderma*, *robertsorum*, and *siopela*. The skull is moderately well ossified. The frontoparietals are widely separated medially throughout their lengths, and a large frontoparietal fontanelle is present (fig. 236). The quadratojugal is reduced or absent; the maxillary does not articulate with the quadratojugal. The anterior arm of the squamosal does not extend more than one-half of the distance

to the maxillary; the posterior arm of the squamosal is short, and the ventral arm is robust. The pterygoid is robust, and the medial ramus articulates with the prootic. The prevomers are unusually small and delicate. Teeth are present on the maxillary, premaxillary, and prevomer. Those on the maxillary and premaxillary are rather long, bifid, and moderately spatulate; some of the teeth on



FIG. 233. Hands of species in the *Hyla bistincta* group. A. *H. bistincta*, K.U. No. 68077. B. *H. pentheter*, K.U. No. 100932. C. *H. robertsorum*, K.U. No. 71266. D. *H. pachyderma*, U.S.N.M. No. 115028. E. *H. siopela*, K.U. No. 100981. F. *H. crassa*, U.I.M.N.H. No. 25050.  $\times 4$ .





FIG. 234. Hands and feet of species in the *Hyla bistincta* group. A and E. *Hyla charadricola*, K.U. No. 58414. B and F. *Hyla chryses*, K.U. No. 106306. C. *Hyla bistincta*, K.U. No. 68077. D. *Hyla pentheter*, K.U. No. 100932.  $\times 4$ .

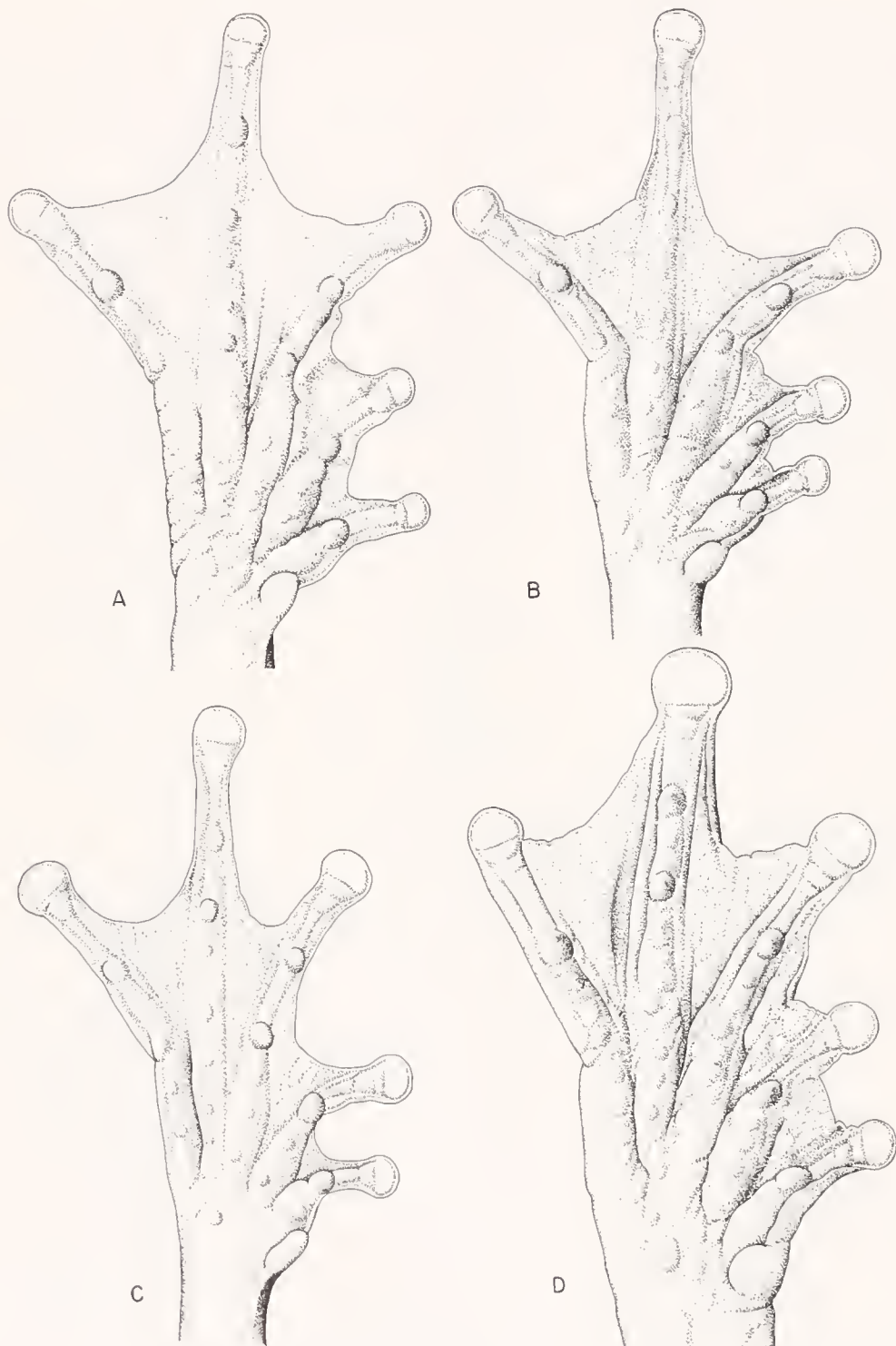


FIG. 235. Feet of species in the *Hyla bistincta* group. A. *H. robertsoni*, K.U. No. 71266. B. *H. pachyderma*, U.S.N.M. No. 115028. C. *H. siopela*, K.U. No. 100981. D. *H. crassa*, U.I.M.N.H. No. 25050.  $\times 4$ .



the premaxillary and anterior part of the premaxillary are hooked. The prevomerine teeth are spatulate and bifid. The tadpoles have a long, terminally rounded tail and a small ventral mouth with lateral folds, two complete rows of fringing papillae and at least one additional irregular row medially, and two upper and three lower rows of teeth (figs. 237 and 238). Only one species, *bistincta*, is known to have a voice; the other species usually lack vocal slits. The haploid number of chromosomes is 12 (known only in *pentheter* and *robertsorum*).

**COMPOSITION:** Nine species (*H. bistincta*, *bogertae*, *crassa*, *charadricola*, *chryses*, *pachyderma*, *pentheter*, *robertsorum*, and *siopela*) comprise this group, which is endemic to the Mexican highlands. All of the species, as now recognized, are monotypic. Of the nine species, 386 preserved frogs, 15 skeletons, and eight lots of tadpoles were examined.

**COMMENTS:** Duellman (1964b) included five species in the *bistincta* group. Adler (1965) named *chryses* and *pentheter* and included them in the *bistincta* group. Duellman (1968a) named *siopela* in the group, and Straughan and Wright (1969) named *bogertae*.

Members of the *Hyla bistincta* group inhabit mountain streams, and the evolutionary trend within the group is towards more aquatic habits in the adults. The tadpoles are moderately well-adapted for development in streams, but they show no advanced specializations. *Hyla bistincta*, the least specialized frog in the group, has relatively short fingers with a moderate amount of webbing, a high, truncate snout, and vocal slits.

*Hyla charadricola* and *chryses* apparently are closely related and represent a divergence from the main evolutionary line within the group. These two species have relatively thinner skin on the dorsum, more slender bodies, an axillary membrane; furthermore, breeding males apparently lack nuptial excrescences. Both species lack vocal slits.

Of the remaining species in the group, *pentheter* most closely resembles *bistincta*, but differs in having longer fingers and usually no vocal slits. The other five species in the group (*bogertae*, *crassa*, *pachyderma*, *robertsorum*, and *siopela*) are the most advanced. They

have short, blunt heads, thick glandular skin, long fingers with little webbing, large webbed feet, nuptial excrescences in breeding males, and no vocal slits or axillary membranes (table 44).

The frogs in the *Hyla bistincta* group present a classic picture of montane distribution. The most primitive species is the most widespread and is the only one that occurs sympatrically with other species in the group. *Hyla chryses* occurs in the Sierra Madre del Sur in Guerrero, and *charadricola* occurs in the high mountains of Hidalgo. *Hyla pentheter* lives in the Sierra Madre del Sur in Oaxaca whereas *robertsorum*, *pachyderma*, *siopela*, and *crassa* occur in that order from north to south in the Sierra Madre Oriental, and *bogertae* occurs in the Sierra Madre del Sur of Oaxaca. Each of the last four species is known from a single stream.

Frogs in the *Hyla bistincta* group presumably are closely related to those of *Plectrohyla*, inhabitants of montane streams in Nuclear Central America. The two groups of species are alike in the absence of a quadratojugal, presence of thick, glandular skin, structure and form of the tadpoles, and in general appearance. They show parallel progressive modifications for a stream existence in the lengthening of the fingers, reduction of webbing on the hand, and loss of vocal slits and a voice. The species in both groups have a broad, ossified prepollex; in *Plectrohyla*, the prepollex has one or more projecting spines. *Plectrohyla* is singularly distinctive in having robust premaxillaries with bifurcate alary processes.

### *Hyla bistincta* Cope

*Hyla bistincta* Cope, 1877, p. 87 [holotype, U.S.N.M. No. 32261 from "most probably Veracruz," México; Francis Sumichrast collector; type locality restricted to Acultzingo, Veracruz, México, by Smith and Taylor (1950, p. 346)]. Brocchi, 1882, p. 43. Boulenger, 1882a, p. 401. Günther, 1901 (1885-1902), p. 265. Kellogg, 1932, p. 163. Smith and Taylor, 1948, p. 87. Duellman, 1964b, p. 475.

*Hyla bistincta labeculata* Shannon, 1951, p. 470 [holotype, U.S.N.M. No. 123689 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector].

*Hyla bistincta bistincta*: Shannon, 1951, p. 472.

**DIAGNOSIS:** *Hyla bistincta* is a moderately large species with a truncate snout in dorsal

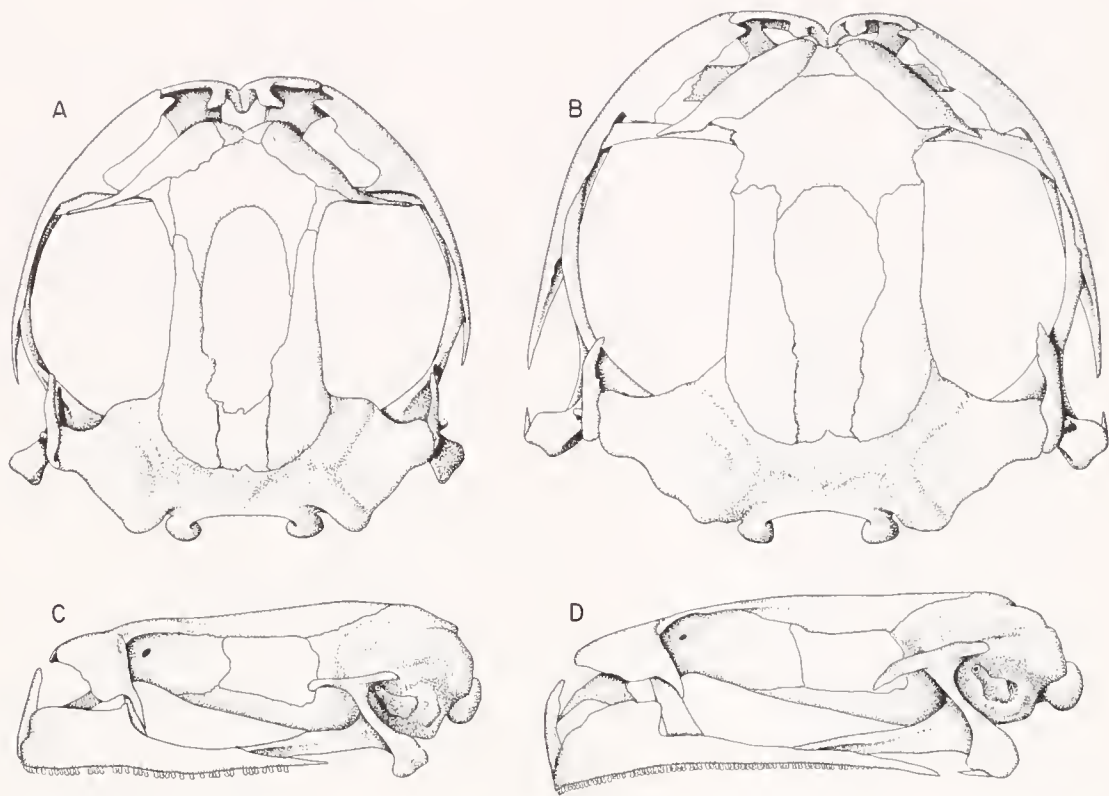


FIG. 236. Dorsal and lateral views of the skulls of two species in the *Hyla bistincta* group. A and B. *H. charadricola*, K.U. No. 55624. C and D. *H. siopela*, K.U. No. 117428.  $\times 5$ .

TABLE 44

Comparison of Sizes and Certain Proportions, with Means in Parentheses, of Males of the Species in the *Hyla bistincta* Group.

Species	N	Snout-vent Length	Tibia Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
<i>H. bistincta</i> .....	38	43.0-53.8 (46.3)	0.470-0.520 (0.490)	0.320-0.370 (0.340)	0.350-0.480 (0.420)
<i>H. pentheter</i> .....	7	43.3-52.1 (46.2)	0.502-0.525 (0.514)	0.350-0.381 (0.367)	0.520-0.586 (0.555)
<i>H. charadricola</i> .....	10	35.3-44.4 (40.4)	0.500-0.540 (0.520)	0.310-0.330 (0.320)	0.300-0.370 (0.340)
<i>H. chryses</i> .....	3	36.3-37.3 (37.1)	0.494-0.498 (0.496)	0.313-0.327 (0.320)	0.595-0.634 (0.574)
<i>H. robertsororum</i> .....	24	39.9-47.9 (43.1)	0.480-0.510 (0.490)	0.300-0.360 (0.320)	0.360-0.470 (0.410)
<i>H. pachyderma</i> .....	1	39.9	0.530	0.320	---
<i>H. siopela</i> .....	7	42.1-46.2 (44.4)	0.472-0.500 (0.487)	0.291-0.317 (0.309)	0.363-0.468 (0.438)
<i>H. crassa</i> .....	1	53.7	0.500	0.330	0.438
<i>H. bogertae</i> .....	1	44.9	0.508	0.369	0.319



FIG. 237. Tadpoles of the species in the *H. bistincta* group. A. *H. pentheter*, K.U. No. 104142. B. *H. bistincta*, U.M.M.Z. No. 115231. C. *H. robertsoni*, K.U. No. 60078. D. *H. siopela*, K.U. No. 100118. A.,  $\times 4$ ; other,  $\times 2$ .

profile. The fingers are short and about one-third webbed; the toes are about two-thirds webbed. A strong tarsal fold is present, but a thoracic fold and axillary membrane are absent. The anal opening is at the level of the ventral surfaces of the thighs. Vocal slits and nuptial excrecences are present. The flanks and posterior surfaces of the thighs are creamy tan with brown reticulations or spots. *Hyla pentheter* resembles *bistincta* but differs in having longer fingers with less webbing and by lacking vocal slits and reticulations on the posterior surfaces of the thighs. *Hyla siopela* differs in having a vertical rostral keel, less webbing, and no vocal slits. Other members of the *Hyla bistincta* group either have thinner, less glandular, skin and an axillary membrane and no nuptial excrecences, or they have round snouts in dorsal profile and long

fingers with little or no webbing. Aside from members of this group, *bistincta* cannot be confused with any other Middle American hylids, except *Plectrohyla*.

**DESCRIPTION:** This is a moderate-sized species of the *Hyla bistincta* group; males attain a maximum snout-vent length of 53.8 mm. and females reach 67.6 mm. In a series of 19 males from Uruapan, Michoacán, México, the snout-vent length is 43.0 to 48.7 (mean, 45.9) mm.; the ratio of tibia length to snout-vent length is 0.470 to 0.515 (mean, 0.492); the ratio of foot length to snout-vent length is 0.425 to 0.485 (mean, 0.452); the ratio of head length to snout-vent length is 0.289 to 0.323 (mean, 0.306); the ratio of head width to snout-vent length is 0.317 to 0.364 (mean, 0.342), and the ratio of the diameter of the tympanum to that of the eye is 0.339



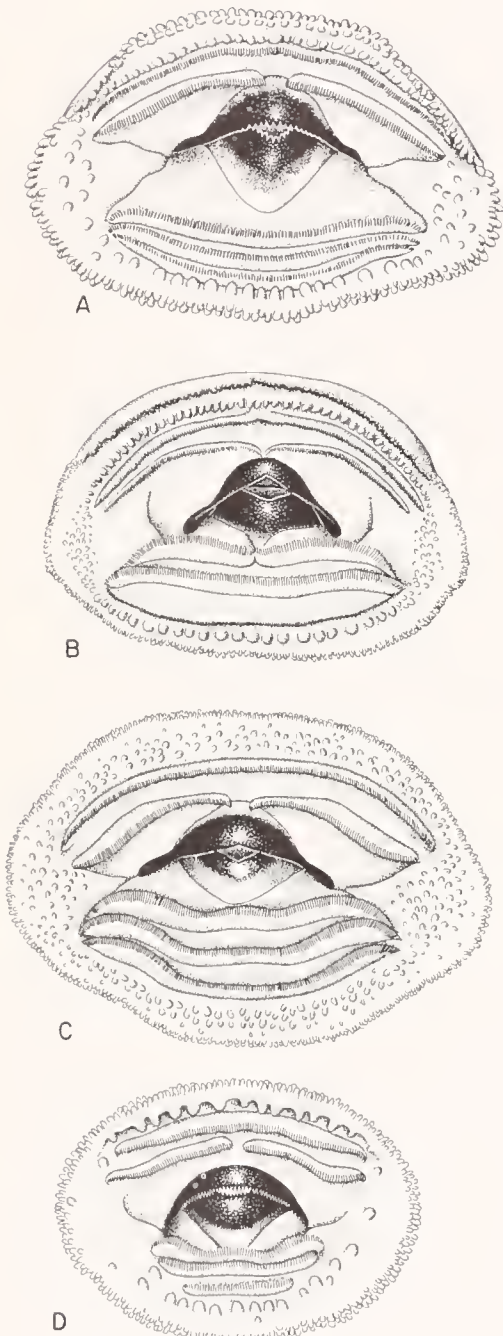


FIG. 238. Mouths of tadpoles of the species in the *H. distincta* group. A. *H. pentheter*, K.U. No. 104142. B. *H. distincta*, U.M.M.Z. No. 115231. C. *H. robertsoni*, K.U. No. 60078. D. *H. siopela*, K.U. No. 110118. A.,  $\times 20$ ; others,  $\times 10$ .

to 0.479 (mean, 0.422). Two females from the same locality have snout-vent lengths of 43.8 and 51.4 mm.; in these specimens the ratio of the diameter of the tympanum to that of the eye is 0.440 and 0.420, respectively.

The head is as wide as, or slightly wider than, the body; the top of the head is slightly convex, and the eyes are large. In dorsal profile the snout is truncate; in lateral profile it is bluntly rounded. The snout is moderately short; the nostrils are barely protuberant and are at a point about two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded, the loreal region is slightly concave, and the lips are thick and barely flared. A heavy dermal fold extends posteriorly from the eye above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long and robust; an abbreviated axillary membrane is present. A few small tubercles are present on the ventral surface of the forearm, but these do not form a distinctive row along the ventrolateral edge of the forearm. A heavy transverse dermal fold is present on the wrist. The fingers are moderately short and stout and bear moderately large discs; the disc on the third finger is about equal in size to the tympanum. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are rather large and round; they are arranged in a single row on the proximal segments of each digit. The outer palmar tubercle is low and rounded; in most specimens it is bifid or tripartite, and in some it is fragmented into one large and one or two small tubercles. An elongate tubercle is present on the prepollex, which is greatly enlarged. Nuptial excrecences, in the form of minute spinules are present on the prepollex, inner edge of the thumb, and inner edge of the second finger in breeding males. The webbing is vestigial between the first and second fingers and extends from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger (fig. 233A). The hind limbs are mod-



erately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A transverse dermal fold is present on the heel, and the tarsal fold is moderately strong and extends the full length of the tarsus. The inner metatarsal tubercle is large, elliptical, and has a raised median edge. The outer metatarsal tubercle is small, and conical. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are large, round, and subconical. The supernumerary tubercles are large, low, and arranged in a single row on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 234C). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed ventrally at the level of the ventral surfaces of the thighs in males and at the level of the middle of the thighs in females. The anal tube is long and curved downward. The skin on the ventral surfaces of the body and thighs is granular; elsewhere the skin is smooth. The tongue is broadly cordiform, shallowly notched behind, and free posteriorly for about one-fourth of its length. The prevomerine teeth are situated on small, high, transverse elevations between the small, ovoid choanae. Males have three to seven teeth on each prevomerine process and a total of six to 14 (mean, 9.8) teeth. Females have five to seven teeth on each process and a total of 10 to 13 (mean, 11.5) teeth. The vocal slits are situated along the inner edge of each ramus of the lower jaw. The vocal sac is single, median, subgular, and barely distensible.

The general coloration of *Hyla bistincta* is pale tan to dark brown dorsally with creamy yellow flanks with brown spots or reticulations (pl. 62, figs. 1 and 2). The posterior surfaces of the thighs are tan or brown with faint yellow spots. The flanks are cream with bold

or fine dark reticulations that tend to enclose yellow spots. The ventral surfaces are a pale yellow. The iris is a pale copper color.

There is considerable variation in color in the living frogs. The dorsum varies from greenish tan to pale yellowish tan to reddish brown, and in some individuals, dark chocolate brown. In the series of specimens from Uruapan, Michoacán, México, the coloration of the flanks and the anterior surfaces varies from nearly uniform creamy yellow with only fine dark reticulations to bold reticulations enclosing yellow spots. In some specimens from Oaxaca and Veracruz, the markings on the flanks consist of irregular spots or dashes, instead of reticulations.

In preservative, the dorsum is various shades of brown, and the ventral surfaces are creamy white. The flanks and anterior surfaces of the thighs are creamy white with dark brown reticulations, and the posterior surfaces of the thighs are tan or brown with creamy white spots.

**TADPOLES:** Duellman (1961c, p. 47) presented a description of the tadpoles of this species from Uruapan, Michoacán, México. Tadpoles are available in developmental stages 25 through 36; the smallest tadpole has a total length of 33.0 mm., and the largest (developmental stage 36) has a total length of 61.0 mm. A typical tadpole in developmental stage 34 has a body length of 19.4 mm. and a total length of 57.6 mm. The body is moderately depressed, as wide as deep. In dorsal profile the snout is broad and rounded; in lateral profile the snout is rounded. The nostrils are small, directed anteriorly, and situated about midway between the eyes and the tip of the snout. The eyes are small and directed dorsolaterally. The spiracle is sinistral; its opening is on the midline at a point about two-thirds of the distance from the snout to the posterior edge of the thighs. The anal tube is short and dextral. The tail is about twice as long as the body with heavy musculature and relatively shallow fins. The caudal musculature does not extend to the tip of the tail. At midlength of the tail, the depth of the musculature is about equal to that of either the dorsal or ventral fin. The dorsal fin extends onto the body. Terminally, the caudal fins are rounded (fig. 237B).

In preservative the body is pale grayish brown dorsally and laterally and pale gray ventrally. The caudal musculature is brown and the fins are translucent with scattered melanophores. The color in life is not known.

The mouth is ventral and moderately large; its width is equal to about two-thirds of the greatest width of the body. The lips are folded laterally; two rows of small papillae completely border the lips. A row of larger papillae is present between the upper lips and the first upper row of teeth, and a similar row is present between the lower lips and the third lower row of teeth. Laterally, these rows of large papillae degenerate into small papillae in the lateral fold. The beaks are moderately robust and bear small peg-like serrations which are slightly larger on the lower beak. The upper beak is a broad arch with short, rounded lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are nearly equal in length and slightly longer than the lower rows, which are subequal in length. The second upper tooth row is narrowly interrupted medially in all specimens, and the first lower row is interrupted in about half of the specimens (fig. 238B).

**MATING CALL:** No recordings of the call of *Hyla bistincta* exist. Shannon (1951, p. 473) remarked that the type specimen of *Hyla bistincta labeculata* was singing when caught. At Uruapan, Michoacán, I heard a low growl-like call that possibly was produced by *Hyla bistincta*, but I did not trace the call to a frog.

**NATURAL HISTORY:** *Hyla bistincta* is an inhabitant of pine-oak, pine-fir, and pine forests in the high mountains of México. Individuals usually are found near streams. At Uruapan and at Dos Aguas, Michoacán, individuals were found by day clinging to roots and vines in heavily shaded areas immediately over cascading streams. At night, the frogs were sitting on rocks and low vegetation near the stream.

Tadpoles were found in gravel-bottomed pools in torrential streams. A recently metamorphosed individual has a snout-vent length of 24.8 mm.

**REMARKS:** Duellman (1964b, p. 477) demonstrated that *Hyla bistincta labeculata* was an unrecognizable subspecies. He reported that in general, specimens from western México have reticulate mottling on the flanks as compared with the marbling on the flanks in specimens from eastern México. The subspecies, *labeculata* was diagnosed by Shannon (1951, p. 470) as differing from the nominate subspecies by having "the gray reticulations of the sides entirely broken up into elongate black blotches; tarsal fold moderately elevated."

Smith and Williams (1963, p. 23) reported a specimen of *Hyla bistincta* from San Vicente, Oaxaca. Duellman (1964b, p. 477) included this record in his account of *Hyla bistincta*. Examination of that specimen (U.I.M.N.H. No. 51346) revealed that it is a poorly preserved specimen of *Hyla pinorum*. Duellman (1964b, p. 478) also included a specimen (A.M.N.H. No. 13447) from Pluma Hidalgo, Oaxaca, in *Hyla bistincta*. Re-examination of that specimen reveals that it is a small individual of *Hyla pentheter*.

**ETYMOLOGY:** The specific name *bistincta* is derived from the Latin *bis* meaning twice and from the Latin *tinctus*, meaning paint or color; the name refers to the distinctive darker coloration of the flanks as compared with the paler dorsum.

**DISTRIBUTION:** *Hyla bistincta* occurs at elevations from 1400 to 2800 meters in the mountains of the Sierra Madre Occidental in southwestern Durango southward through the Cordillera Volcánica in Michoacán, México, and Morelos, in the Sierra de Coaleomán in Michoacán, and in the Sierra Madre del Sur in Guerrero; this species also occurs in the Sierra Madre Oriental from central Veracruz to central Oaxaca (fig. 239).

See Appendix 1 for the locality records of the 114 specimens examined.

### *Hyla pentheter* Adler

*Hyla pentheter* Adler, 1965, p. 5 [holotype, U.M.M.Z. No. 125381 from 37 kilometers north (by road) of San Gabriel Mixtepec, Oaxaca, México, elevation 1860 meters; Kraig Adler collector].

**DIAGNOSIS:** This is a moderately large species with a truncate snout in dorsal profile, thick, glandular skin, long fingers with



FIG. 239. Distribution of *Hyla bistincta* and *Hyla pentheter*.

only vestigial webbing, a distinct tarsal fold, anal opening at level of ventral surfaces of thighs, and nuptial excrescences present in breeding males. *Hyla pentheter* lacks vocal slits, axillary membranes, and a thoracic fold. The dorsum is pale tan, yellow, or gray. The sides of the head, flanks, and inner and outer edges of the limbs are dark brown. *Hyla bistincta* resembles *pentheter* but differs by having vocal slits, shorter fingers that are about one-third webbed, and reticulations or spots on the flanks and posterior surfaces of the thighs. *Hyla siopela* has a vertical rostral keel and no dark brown color on the sides of the body. Other species in the *Hyla bistincta* group either have thinner, less glandular skin, an axillary membrane, and no nuptial excrescences, or they have round snouts in dorsal profile. The only other Middle American hy-

lids with which *pentheter* can be confused are species of *Plectrohyla*.

**DESCRIPTION:** This is a moderately large species; males attain a maximum snout-vent length of 52.1 mm., and females reach 56.4 mm. In a series of seven males from the Pacific slopes of the Sierra Madre del Sur in Oaxaca, México, the snout-vent length is 43.3 to 52.1 (mean, 46.2) mm.; the ratio of tibia length to snout-vent length is 0.502 to 0.525 (mean, 0.514); the ratio of foot length to snout-vent length is 0.431 to 0.460 (mean, 0.447); the ratio of head length to snout-vent length is 0.350 to 0.381 (mean, 0.367), and the ratio of the diameter of the tympanum to that of the eye is 0.520 to 0.586 (mean, 0.555). Two females from the same area have snout-vent lengths of 56.0 and 56.4 mm. They show no differences in proportions from the males.



The head is as wide or slightly wider than the body, and the top of the head is flat. In dorsal profile the snout is truncate; in lateral profile it is acutely angular just anterior to the nostrils and barely rounded at the margin of the lip. The snout is short; the nostrils are slightly protuberant and situated about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is slightly concave, and the lips are thick and flaring. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to the point of insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arms are moderately long and robust; no axillary membrane is present. Tubercles are absent from the ventrolateral edge of the forearms, but a distinct transverse dermal fold is present on the wrist. The fingers are long and moderately slender and bear rather large discs; the disc on the third finger is slightly smaller than the diameter of the tympanum. The subarticular tubercles are large, round, flat on the third and fourth fingers, and conical on the first and second. The supernumerary tubercles are large, conical, and arranged in a single row on the proximal segments of each digit. None of the tubercles is bifid. A large, flat, bifid palmar tubercle is present, and an elongate tubercle is present on the prepollex. The prepollex is greatly enlarged, and in breeding males bears a nuptial excrescence composed of minute spinules; spinules are present on the inner surfaces of the thumb and second finger. A vestige of a web is present between the first and second and third fingers, whereas the web extends from the base of the antepenultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth finger (fig. 233B). The hind limbs are moderately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A faint transverse dermal fold is present on the heel, and the tarsal fold, which is indistinct in some specimens, extends the full length of the tarsus.

The inner metatarsal tubercle is large, ovoid, elevated, and barely visible from above. The outer metatarsal tubercle is small and conical. The toes are long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are large and conical; the supernumerary tubercles are small, conical, and arranged in a single row on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 234D). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed ventrally at the midlevel of the thighs; a long anal sheath is present. The skin on the ventral surfaces of the body and posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is broadly cordiform, shallowly notched posteriorly and barely free behind. The denticulate processes of the prevomers are short transverse ridges between the small, round choanae. Males have three to six teeth on each process and have a total of seven to 11 (mean, 8.7) teeth. Females have six to eight teeth on each process and a total of 13 to 15 (mean, 14.0) teeth. Vocal slits are absent in most specimens.

The general coloration of *Hyla pentheter* is grayish brown or yellowish brown above with dark brown on the sides of the head, body, and limbs (pl. 62, figs. 3 and 4). The dorsum is uniformly colored and varies from a pale grayish brown to yellowish tan or yellow with a slight greenish tinge. A broad, dark, chocolate brown band extends from the edge of the upper lip below the nostril to the eye, along the supratympanic fold and the side of the body. The flanks are dark brown with yellow spots. The anterior and posterior surfaces of the thighs, outer edges of the shanks and feet, and ventrolateral edges of the forearm are dark brown. Large yellow spots are present on the anterior and posterior surfaces of the thighs. The venter is yellow,



darkest on the throat and chest. The throat is mottled with olive-brown in some specimens. The iris is reddish copper with black reticulations, and the palpebrum is clear. The nuptial excrescences are dark brown.

Adler (1965, p. 8) stated: "Metachrosis is moderate. When the dorsum is light grayish tan (pl. IE) the brown band along the side of the body is bordered above by a thin whitish-tan line." This line was evident in living specimens of all colors, but was most prominent in those individuals having a darker dorsum. In some specimens having grayish brown or yellowish tan dorsal color, small dark brown flecks are evident on the dorsum.

In preservative, the dorsum is gray or dull brown with or without small brown flecks. The venter is creamy yellow. The dark lateral markings are black or dark brown; and the spots on the flanks are dull yellow.

**TADPOLES:** A series of tadpoles in developmental stages 25 to 27 are available from a small stream 37 kilometers north of San Gabriel Mixtepec, Oaxaca, México. A typical tadpole in developmental stage 25 has a body length of 9.2 mm. and a total length of 26.4 mm. The body is as wide as deep, only moderately depressed. In dorsal profile the snout is bluntly rounded; in lateral profile it is gently rounded. The nostrils are small, directed anterodorsally, and situated slightly closer to the eyes than to the tip of the snout. The eyes are small and directed dorsolaterally. The spiracular opening is directed posterodorsally just below the midline at a point about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The tail is about twice as long as the body and is shallow. The caudal musculature is moderately deep and does not extend to the tip of the tail. At midlength of the tail, the depth of the musculature is slightly less than the depth of either the dorsal or ventral fin. The dorsal fin barely extends onto the body and is deepest just posterior to the midlength of the tail. The ventral fin is of equal depth throughout its length; terminally the fins are pointed (fig. 237A).

The body is dark brown with greenish yellow flecks dorsally, golden flecks laterally and white flecks ventrally. The dorsal edge of the caudal musculature is dark brown and

orange. The fins are transparent with faint brown flecks. The iris is bronze. In preservative, the body and caudal musculature are pale creamy tan. The top of the body, a small area anteroventral to the eye, and a large blotch on the side of the body posterior to the eye are dark brown. The dorsal edge of the caudal musculature is dark brown. Small brown flecks are scattered on the caudal musculature and on the dorsal fin.

The mouth is ventral; its width is equal to about two-thirds the width of the body. A lateral fold is present in the lips. Two rows of small papillae border the lip anteriorly and posteriorly, and a single row is present laterally. A row of larger papillae is present between the fringing papillae and the first upper tooth row, and a row of large papillae is present between the fringing papillae and the third lower tooth row; laterally in the lateral fold the large papillae degenerate into scattered smaller papillae. The beaks are robust and bear large, blunt serrations. The upper beak forms a broad arch with laterally directed, short, blunt, lateral processes. The lower beak is V-shaped. There are two upper and three lower rows of teeth. The upper rows are about equal in length and slightly longer than the lower rows. The second upper row is narrowly interrupted medially (fig. 283A).

**MATING CALL:** As indicated by the absence of the vocal slits, this species apparently lacks a voice.

**NATURAL HISTORY:** *Hyla pentheter* inhabits humid montane pine-oak forest, where it lives in the vicinity of cascading mountain streams. Adler (1965, p. 8) found a female "in the afternoon on the forest floor near the base of a cliff, a dozen meters from the nearest stream." He found males on vines and twigs or on moss-covered boulders near or over the stream. At the type locality, I obtained individuals of both sexes from low trees near a stream at night, and one male was found on a boulder in the stream. One individual was found on a boulder in a stream 29 kilometers south-southeast of Juchatengo, Oaxaca.

The tadpoles were found in a pool in the stream, where they laid quietly on the bottom, but when disturbed took refuge on the bottom in the leaf litter.

**REMARKS:** Duellman and Cole (1965, p.

141) reported the number of chromosomes in *Hyla bistincta*. Re-examination of the specimens from which the chromosome preparations were made proves that it is an example of *Hyla pentheter*. A faded juvenile (A.M.N.H. No. 13447) from Pluma Hidalgo, Oaxaca, was listed as *Hyla bistincta* by Duellman (1964, p. 478).

**ETYMOLOGY:** The specific name *pentheter* is Greek, meaning mourner and is used in allusion to the black border of the body, a symbol of mourning.

**DISTRIBUTION:** *Hyla pentheter* is known only from elevations between 1500 and 2000 meters on the Pacific slopes of the Sierra Madre del Sur in southern Oaxaca, México (fig. 239).<sup>13</sup>

See Appendix 1 for the locality records of the 12 specimens examined.

### *Hyla charadricola* Duellman

*Hyla charadricola* Duellman, 1964b, p. 478 [holotype, K.U. No. 58414 from the Río Totolapa, 14.4 kilometers (by road) west of Huachinango, Puebla, México, elevation 2280 meters; John Wellman collector].

**DIAGNOSIS:** This is a medium-sized species (maximum snout-vent length in males, 44.4 mm.) with a truncate snout, relatively thin skin on the dorsum, and an axillary membrane. The dorsum is olive-green with black reticulations, and the flanks are grayish green with brown spots. Vocal slits, nuptial excrescences, and a thoracic fold are lacking, and the anal opening is at the level of the middle of the thigh. The foregoing combination of characters distinguishes *charadricola* from other members of the *Hyla bistincta* group, of which *chryses* most closely resembles *charadricola*. The former differs by having a pointed snout in dorsal profile, larger tympanum in relation to the eye (mean ratio, 0.574, as compared with 0.340 in *charadricola*), and a golden yellow dorsum in life. Superficially *Hyla charadricola* resembles *miotympanum* and *arborescendens*, both of which have round snouts and shorter fingers.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 44.4 mm., and females reach 50.9 mm. In a series of 10 males from Río Totolapa, 14.4 kilometers west of Huachinango, Puebla, México, the snout-vent length is 35.3 to 44.4 (mean, 40.4) mm.; the ratio of tibia length to snout-vent length is 0.500 to 0.535 (mean, 0.517); the ratio of foot length to snout-vent length is 0.459 to 0.506 (mean, 0.493); the ratio of head length to snout-vent length is 0.292 to 0.319 (mean, 0.308); the ratio of head width to snout-vent length is 0.311 to 0.334 (mean, 0.320), and the ratio of the diameter of the tympanum to that of the eye is 0.295 to 0.372 (mean, 0.340). Three females from the same locality have snout-vent lengths of 43.4 to 50.9 (mean, 48.1) mm. The tympanum is slightly larger in females than in males; the ratio of the diameter of the tympanum to that of the eye in females is 0.375 to 0.391 (mean, 0.384).

The head is as wide as the body; the top of the head is flat. The eyes are large and prominent. In dorsal profile, the snout is truncate; in lateral profile, it is bluntly rounded. The snout is short; the nostrils are slightly protuberant and situated about three-fourths the distance from the eyes to the tip of the snout. The internarial region is slightly depressed. The canthus is rounded; the loreal region is barely concave, and the lips are thick and flaring. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which is barely distinct and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arms are moderately long and slender; a distinct axillary membrane is present. A row of low tubercles is present on the ventral edge of the forearm, and a faint transverse dermal fold is present on the wrist. The fingers are long and slender and bear relatively small discs; the width of the disc on the third finger is less than the diameter of the tympanum. The subarticular tubercles are small and round; the supernumerary tubercles are small, subconical, and irregularly placed on the proximal segments of the second, third, and fourth fingers. The palmar

<sup>13</sup> Dr. Robert G. Webb obtained one specimen of this species on July 22, 1968, at 11 kilometers south of Chicahuaxtla, Oaxaca, at an elevation of 1450 meters. Dr. Kraig Adler obtained five individuals from three localities in the mountains west of Chilpancingo, Guerrero, in December, 1969.

tubercle is flat and is usually bifid. The prepollex is greatly enlarged, flattened, and ovoid; nuptial excrescences are absent in breeding males. A vestige of webbing is present between the second and third and the third and fourth fingers (fig. 234A). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A moderately heavy transverse dermal fold is present on the heel. The tarsal fold is weak and usually present only on the distal half of the tarsus. The inner metatarsal tubercle is moderately large, ovoid, flattened, and raised medially. The outer metatarsal tubercle is small and conical. The toes are long and slender and bear discs that are about equal to the size of those on the fingers. The subarticular tubercles are small and round, and the supernumerary tubercles are minute and subconical. The toes are three-fourths webbed (fig. 234E). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroven- trally at the midlevel of the thighs. A short, thin anal sheath is present. The skin on the belly and proximal posteroventral surfaces of the thighs is weakly granular; no thoracic fold is present. The skin on the other surfaces is smooth. The tongue is nearly round, shallowly notched behind, and free posteriorly for about one-fourth of its length. The dentic- erous processes of the prevomer are narrow transverse ridges between the moderately large, round choanae. Males have two to five teeth on each process and a total of five to 10 (mean, 7.6) prevomerine teeth. Females have four or five teeth on each process and a total of eight to 10 (mean, 9.0) prevomerine teeth. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla charad- ricola* is dark green with darker green reticu- lations on the back (pl. 63, fig. 1). The dorsal

surfaces of the head, body and limbs are dark green; darker green reticulations usually are evident on the back. The flanks are dirty white with dark olive-gray mottling. A dark olive-gray stripe extends from the nostril to the eye and then to the insertion of the arm. The upper lips are pale green. The inguinal region, anterior and posterior surfaces of the thighs, and inner surfaces of the feet are dark yellowish orange. The ventral surfaces of the shanks, feet, and webbing are dusty yellow. The belly is white, and the iris is silvery gold.

In some individuals, the dark reticulations on the dorsum are faint. Some adults, when collected, were pale green with faint or no dorsal reticulations; later these individuals became darker, and usually the reticulations were evident. In all specimens the anal stripe is absent and the flanks are heavily mottled. Juveniles have a dorsal color varying from rich brown with darker reticulations to pale green or gray with dark green reticulations.

In preservative the dorsum is purplish brown with fine darker reticulations on the back. The flanks are pale tan with dark brown spots, and the posterior surfaces of the thighs are tan. The chin is creamy white with brown spots, and the belly is dusty white. The ven- tral surfaces of the thighs and shanks are pale yellow; the webbing is grayish brown. The ventral surfaces of the first two fingers are dusty white, and the ventral surfaces of the third and fourth fingers and of the feet are brown. There is no anal stripe, but small white flecks are present above and below the anal opening.

**TADPOLES:** The tadpoles of *Hyla charad- ricola* are unknown. Presumably, they devel- op in mountain streams.

**MATING CALL:** The absence of vocal slits and a vocal sac precludes the presence of a call in this species.

**NATURAL HISTORY:** Most specimens were obtained at the Río Totolapa, a shallow rocky stream in a pine forest. There, *Hyla charad- ricola* was found beneath rocks at the edge of fast moving sections of the stream and be- neath rocks in shallow ripples in the stream. Most of the frogs were in water. At night, they were found sitting on rocks in the stream. At Lago de Tejocotal, *Hyla charadricola* was found beneath rocks at the shore of the lake



and by a stream in the pine forest. Individuals were found on low vegetation overhanging a small stream in pine-oak forest, 4 kilometers southwest of Tianguistengo, Hidalgo, México.

*Hyla miotympanum* is abundant at the Río Totolapa. Individuals of this species were found beneath rocks at the edge of the stream by day and in bushes along the stream at night, but not in the ripples inhabited by *Hyla charadricola*.

Five recently metamorphosed young were found at the Río Totolapa, on June 8, 1960; these specimens have snout-vent lengths of 22.4 to 24.0 (mean, 23.2) mm.

REMARKS: The presence of an axillary membrane and relatively thin skin on the dorsum, plus the absence of nuptial excrescences in breeding males are characteristics shared by *Hyla chryses*. The latter differs in coloration and in having a pointed, instead of a truncate snout.

ETYMOLOGY: The specific name *charadricola* is derived from the Greek *charadra*, meaning mountain stream, and the Latin suffix, *-cola*, meaning an inhabitant; the name refers to the habitat of the frog.

DISTRIBUTION: *Hyla charadricola* inhabits streams in pine and pine-oak forests at elevations of 2000 to 2300 meters in northern Puebla and in eastern Hidalgo, México (fig. 240).

See Appendix 1 for the locality records of the 59 specimens examined.

### *Hyla chryses* Adler

*Hyla chryses* Adler, 1965, p. 1 [holotype, U.M.M.Z. No. 125374 from between Puerto Chico and Asoleadero (about 45 kilometers airline west-northwest of Chilpancingo), Guerrero, México, elevation 2540-2600 meters; Kraig Adler collector].

DIAGNOSIS: This small (males attain a snout-vent length of 37.3 mm.) member of the *Hyla bistincta* group has relatively thin skin on the dorsum, a pointed snout in dorsal profile, and an axillary membrane. The dorsum is golden yellow to dark greenish brown. Vocal slits, nuptial excrescences, and a thoracic fold are lacking, and the anal opening is at the level of the middle of the thigh. The only other member of the *Hyla bistincta* group having an axillary membrane, thin skin, and

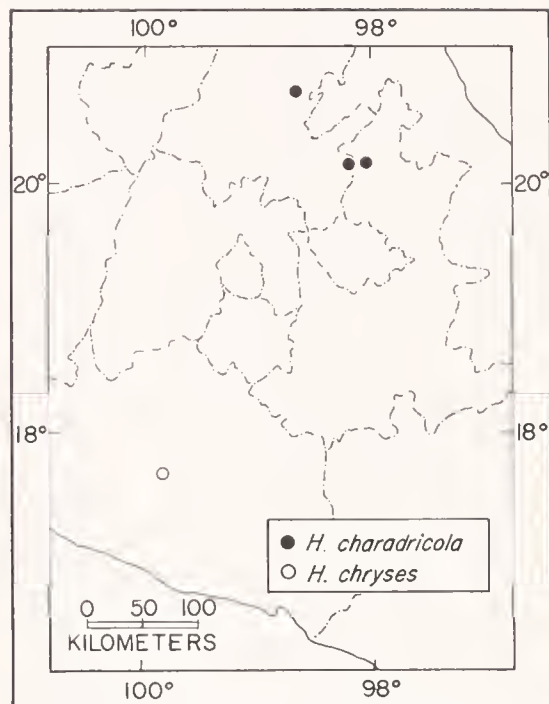


FIG. 240. Distribution of *Hyla charadricola* and *Hyla chryses*.

lacking nuptial excrescences is *charadricola*. That species has a green dorsum, truncate snout in dorsal profile, and a smaller tympanum (mean tympanum/eye ratio 0.340, as compared with 0.574 in *chryses*). Some members of the *Hyla pinorum* and *mixomaculata* groups superficially resemble *chryses*. Members of both groups are smaller and either have blunt snouts or small or covered tympani.

DESCRIPTION: This is the smallest species in the *Hyla bistincta* group. Males attain a maximum known snout-vent length of 37.6 mm., and the one female has a snout-vent length of 42.2 mm. In a series of three males from the type locality in the Sierra Madre del Sur in Guerrero, México, the snout-vent length is 36.3 to 37.6 (mean, 37.1) mm.; the ratio of tibia length to snout-vent length is 0.494 to 0.498 (mean, 0.496); the ratio of foot length to snout-vent length is 0.473 to 0.482 (mean, 0.478); the ratio of head length to snout-vent length is 0.313 to 0.316 (mean, 0.315); the ratio of head width to snout-vent length is 0.313 to 0.327 (mean, 0.320), and



the ratio of the diameter of the tympanum to that of the eye is 0.595 to 0.634 (mean, 0.610). The one female does not differ noticeably in proportion from the males, except that it has a slightly smaller tympanum; the tympanum/eye ratio is 0.574.

The head is as wide as the body; the top of the head is barely convex. The eyes are moderately large and prominent. In dorsal profile, the snout is broadly pointed with a faint imitation of a rostral keel; in lateral profile the snout is bluntly rounded. The snout is moderately long; the nostrils are protuberant and situated about three-fourths of the distance from the eyes to the tip of the snout. The internarial region is barely depressed. The canthus is round; the loreal region is noticeably concave and the lips are thick and barely flared. A moderately heavy dermal fold extends from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and is separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and slender; an indistinct axillary membrane is present. A few low tubercles are present along the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are small, subconical, and irregularly arranged on the proximal segments of the digits. The palmar tubercle is flat and bifid. The prepollex is moderately enlarged and ovoid; nuptial excrescences apparently are lacking in breeding males. The webbing between the fingers is vestigial (fig. 234B). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the middle of the eyes. A weak transverse dermal fold is present on the heel, and a weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is elliptical, rounded, and bare-

ly visible from above. The outer metatarsal tubercle is absent. The subarticular tubercles are moderately large and round. The supernumerary tubercles are small and subconical. The toes are about two-thirds webbed (fig. 234F). The webbing connects the first and second toes at the level of the distal end of the antepenultimate phalanges; the web extends from the base of the penultimate phalanx of the second toe to the base of the antepenultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs and is covered by a short, broad anal sheath. Large tubercles are present ventral and ventrolateral to the anal opening. The skin on the throat, belly, and ventral surfaces of the thighs is granular; elsewhere it is smooth. A thoracic fold is absent. The tongue is narrowly cordiform, shallowly notched behind, and barely free posteriorly. The denticulous processes of the prevomers are small and ovoid; they lie in a transverse plane between the moderately large, round choanae. Males have one to three teeth on each process and a total of three to five (mean, 4.3) prevomerine teeth. The one female has three and four teeth on each process and a total of seven prevomerine teeth. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla chryses* is golden yellow with dark brown flecks above, or dark brown mottled with gray (pl. 62, fig. 2). I have not observed this species in life, so I quote from the type description by Adler (1965, p. 2):

"When cold and sluggish: dorsum of body, head, and limbs, and sides of body dark greenish chocolate brown mottled with dark gray; some metallic green flecking on back, especially evident on dorsal surface of thigh; small metallic green spots along side of body; venter mottled with dark brown and gray. When warmer and more active: dorsum of body, head and limbs, and sides of body metallic golden yellow overlaid with small brown flecks and less numerous indistinct green flecks; area below eye from nostril tube and including tympanum golden; golden pigment below the eye with some brown flecking; can-

thus and supratympanic fold edged with blackish brown; iris chocolate brown overlaid with gold flecking towards center; venter whitish overlaid with brassy flecking and some brown flecks, the brassy pigment most concentrated on throat; undersurfaces of legs with pale yellow wash; whitish pustules on supra-anal flap."

In preservative the dorsum of the body, head, and limbs is dull brownish gray with dark brown or black flecks. The fingers and toes are pale brown with few flecks. The loreal region is dark gray, and the supratympanic fold is dark brown or black. The sides of the body are pale tan mottled with dark brown. The anal pustules are pale grayish tan. The posterior surfaces of the thighs are pale tan with faint brown mottling. The venter is creamy yellow with brown flecks.

Adler (1965, p. 4) stated: "... there is considerable metachrosis in this species. The golden-yellow dorsum has a slight greenish east in some specimens, and in one male there is some black flecking on the back. The pale yellow wash on the undersurface of the legs is absent in one male."

**TADPOLES:** No tadpoles of this species are known. Presumably they develop in mountain streams.

**MATING CALL:** The absence of vocal slits and a vocal sac precludes the presence of a voice in this species.

**NATURAL HISTORY:** Adler (1965, p. 4) stated that the frogs of this species were obtained in "cold, moist, oak-pine-fir cloud forest." He found the frogs by day under loose bark of fallen oak and pine logs in the forest.

**REMARKS:** The presence of relatively thin skin on the dorsum and an axillary membrane, plus the absence of nuptial excrescences in breeding males are characters shared with *Hyla charadriicola*. The latter differs from *chryses* by having a truncate snout and green dorsal coloration.

**ETYMOLOGY:** The specific name is derived from the Greek *Chryses*, one of the priests of Apollo.

**DISTRIBUTION:** *Hyla chryses* is known only from oak-pine-fir forest at elevations between 2540 and 2600 meters in the Sierra Madre del Sur in Guerrero, México (fig. 240).

See Appendix I for the locality records of the four specimens examined.

### *Hyla robertsorum* Taylor

*Hyla robertsorum* Taylor, 1940c, p. 393 [holotype, F.M.N.H. No. 100124 (formerly E.H.T.-H.M.S. No. 16264) from El Chico Parque Nacional, Hidalgo, México; Radclyffe and Hazel Roberts and Edward H. Taylor collectors]. Smith and Taylor, 1948, p. 87. Duellman, 1964b, p. 481.

**DIAGNOSIS:** *Hyla robertsorum* is a moderately large (snout-vent length in males, 47.9 mm.) member of the *Hyla bistincta* group with a bluntly rounded snout, weak thoracic fold, short and weak tarsal fold, vestigial webbing between the long fingers, and small nuptial spines on the prepollex in breeding males. Vocal slits and an axillary membrane are absent. *Hyla robertsorum* is similar to *siopela*, which has a more truncate snout with a weak rostral keel and less webbing on the feet (2/3 in *siopela*; 4/5 in *robertsorum*) and lacks a thoracic fold. *Hyla bogertae* differs from *robertsorum* by having no webbing on the hand and by having olive-green flanks with large yellow spots; furthermore, the belly in *bogertae* is white, instead of gray. *Hyla pachyderma* differs from *robertsorum* by having strong thoracic and tarsal folds and large nuptial spines in breeding males. *Hyla crassa* differs by lacking a thoracic fold and having a strong tarsal fold and by having an anal stripe but no spots below the anal opening; *robertsorum* lacks an anal stripe, but has spots below the opening. *Hyla arborescendens* resembles *robertsorum* but has vocal slits and shorter fingers with more webbing.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 47.9 mm., and females reach 50.8 mm. In a series of 24 males from El Chico Parque Nacional, Hidalgo, México, the snout-vent length is 39.9 to 47.9 (mean, 43.1) mm.; the ratio of tibia length to snout-vent length is 0.480 to 0.510 (mean, 0.490); the ratio of foot length to snout-vent length is 0.459 to 0.515 (mean, 0.495); the ratio of head length to snout-vent length is 0.268 to 0.322 (mean, 0.293); the ratio of head width to snout-vent length is 0.300 to 0.360 (mean, 0.320), and the ratio of the diameter of the tympanum to that of the eye is 0.360 to 0.470 (mean, 0.410). Five fe-

males from the same locality have snout-vent lengths of 47.5 to 50.8 (mean, 49.6) mm. The females do not differ from the males in proportions, except in having a proportionally larger tympanum; the ratio of the diameter of the tympanum to that of the eye in females is 0.420 to 0.553 (mean, 0.462).

The head is narrower than the body; the top of the head is barely convex. In dorsal profile the snout is bluntly rounded; in lateral profile the snout is gently sloped above and rounded below. The snout is short; the nostrils are slightly protuberant and situated about two-thirds of the distance from the eyes to the tip of the snout; the internarial region is slightly depressed. The canthus is rounded, but distinct; the loreal region is concave, and the lips are thick and barely flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and angles downward to a point above the insertion of the arm. From the angle of the supratympanic fold, another heavy fold extends downward to the angle of the jaw. The upper and posterior edges of the tympanum are covered, at least in part, by these dermal folds. The ventral and the anterior edges of the tympanum are distinct; the tympanum is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long and robust; no axillary membrane is present. A few small tubercles are present on the ventrolateral edge of the forearm, and a weak dermal fold is present on the wrist. The fingers are long and slender and bear small discs; the width of the disc on the third finger is slightly less than the diameter of the tympanum. The subarticular tubercles are moderately large and conical; none is bifid. The supernumerary tubercles are large, round, and arranged in a single row on the proximal segments of each digit. A large, elevated, bifid palmar tubercle is present. The prepollex is greatly enlarged and rounded. In breeding males an extensive nuptial excrecence composed of minute spines is present on the prepollex and inner surfaces of the thumb and second finger; in some individuals a few spines are present on the inner surface of the penultimate phalanx of the third finger. There is no web between the first and second fingers and only a rudimentary web between the others (fig. 233C).

The hind limbs are robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A heavy transverse dermal fold is present on the heel. The tarsal fold is weak and usually is present only on the distal half of the tarsus. The inner metatarsal tubercle is moderately large, ovoid, and rounded. The outer metatarsal tubercle is small and subconical. The toes are long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are large and round. The supernumerary tubercles are large, conical, and present in a single row on all but the penultimate and antepenultimate phalanges of each digit. The toes are about four-fifths webbed (fig. 235A). The webbing extends from the base of the disc of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs; it is covered by a short anal sheath. The anal sheath is deeply creased medially. A heavy transverse dermal fold is present above the anus, but large anal tubercles are present. The skin on the proximal posteroventral surfaces of the thighs is granular; that on the belly and chin is areolate, and that on the dorsum and ventral surfaces of the limbs is smooth except for a few small tubercles on the head. A weak thoracic fold is present. The tongue is elliptical and slightly longer than wide; it is free posteriorly for about one-fourth of its length but is not notched behind. The denticulate processes of the prevomers are small transverse ridges that are widely separated and situated between the rather small elliptical choanae. Males have two to four teeth on each process and a total of four to seven (mean, 6.0) prevomerine teeth. Females have two to five teeth on each process and a total of five to nine (mean, 7.0) prevomerine teeth. Vocal slits and a vocal sac are absent.



The general coloration of *Hyla robertsonorum* is dull brown with darker brown reticulations and irregular blotches on the dorsum (pl. 63, fig. 3). The flanks are brown with pale yellow spots; the belly is gray to grayish brown with faint cream spots. The iris is deep bronze.

Some individuals have nearly uniform grayish brown ventral surfaces; in others the chin, as well as the abdomen, is brown with cream spots. The dorsal surfaces of some specimens are nearly uniform dark brown with no reticulations. In others the dorsum is paler brown with distinct darker mottling; in some of these there is little mottling laterally so that there is the effect of an irregular, pale brown, dorsolateral stripe. Some of the largest specimens of both sexes have indistinct cream pustules scattered on the ventral surfaces of the forearms.

In preservative the dorsal surfaces are dark brown with irregular darker reticulations. The flanks are brown with small creamy white spots, and the posterior surfaces of the thighs are dark brown. The chin is creamy tan, and the belly is grayish brown with cream flecks. The ventral surfaces of the limbs are pale brown and the webbing on the feet is gray. Small white spots are present in the anal region.

**TADPOLES:** No tadpoles in advanced developmental stages are available for study; however, specimens are available in developmental stages 25 through 37. The tadpoles in developmental stage 25 have an enormous range in size. The smallest specimen has a body length of 7.8 mm. and a total length of 21.3 mm., whereas the largest individual has a body length of 22.9 mm. and a total length of 59.7 mm. The largest tadpole examined is in developmental stage 37 and has a body length of 26.0 mm. and a total length of 75.2 mm.

A typical tadpole in developmental stage 25 has a body length of 21.8 mm. and a total length of 58.9 mm. The body is depressed and slightly wider than deep. In dorsal profile the snout is bluntly rounded; in lateral profile it is rounded above and truncate anteriorly. The nostrils are small, directed anterolaterally, and situated about midway between the eyes and the tip of the snout. The

eyes are small and directed dorsolaterally. The spiracle is sinistral; its opening is directed posteriorly at a point on the midline at about midlength of the body. The cloacal tube is long and dextral. The tail is long, low, and terminally rounded. The caudal musculature is robust and deep; at midlength of the tail the depth of the musculature is equal to the depth of the ventral fin and greater than the depth of the dorsal fin. The dorsal fin extends onto the body (fig. 237C).

The body is dark grayish brown above and laterally and gray with bluish white flecks below. The caudal musculature is brown, and the fins are tan. Small, round, brown spots are scattered on the caudal musculature and fins. The iris is dull bronze. In preservative, the body is dark brown and the tail is creamy tan with dark brown spots.

The mouth is ventral and moderately large; its width is equal to about two-thirds of the width of the body. Deep lateral folds are present in the lips which are bordered two rows of small papillae, median to which are several irregular rows of somewhat larger papillae. The beaks are moderately robust and bear small peg-like serrations. The upper beak is in the form of a broad arch with long, moderately robust, terminally rounded lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are about equal in length and extend to the papillae laterally; the second upper tooth row is interrupted medially. The lower rows are complete and slightly shorter than the upper rows (fig. 238C).

**MATING CALL:** The absence of vocal slits and a vocal sac preclude the presence of a mating call in this species.

**NATURAL HISTORY:** *Hyla robertsonorum* inhabits fir and pine-fir forests at high elevations. Most specimens have been found along small streams in montane meadows. Taylor (1940c, p. 393) found individuals in plants along spring-fed rivulets in an open meadow at El Chico Parque Nacional, Hidalgo, México. He noted that active frogs dove into the stream and took refuge in the mud on the bottom. Rabb and Mosimann (1955, p. 1) found individuals along the banks of tiny streams in open meadows and noted that the



frogs sought refuge in the water. I have observed the same behavior in *Hyla robertsoni*, but also have found individuals beneath rocks at the edges of streams and on the earthen banks of rivulets in places where dense growths of grasses overhung the streams. Individuals were found sitting on rocks, junipers, and clumps of grasses along the stream at night when the temperature varied from 10° to 14°C.

Tadpoles were found in quiet pools in rivulets in a mountain meadow and in pools in streams in pine forests. The great variation in size of tadpoles in developmental stage 25 and the fact that tadpoles in many stages of development are found in the same pool at the same time suggest that the larval period is prolonged in this species. Possibly the duration of larval development is more than one year.

Four completely metamorphosed juveniles have snout-vent lengths of 30.6 to 32.0 mm.

REMARKS: Many of the specimens of *Hyla robertsoni* are subadults. These specimens can be confused with adults of *Hyla arborescens* and *Hyla charadriicola*. The former has shorter fingers and more webbing and vocal slits. The latter has a more truncate snout, an axillary membrane, and relatively thinner, less glandular skin on the dorsum.

ETYMOLOGY: The specific name is a patronym for Radelyffe and Hazel Roberts, who collected part of the type series.

DISTRIBUTION: *Hyla robertsoni* inhabits streams in the pine and fir forests and montane meadows at elevations of 2250 to 3050 meters in the Sierra Madre Oriental and extreme northern Puebla and eastern Hidalgo, México (fig. 241).

See Appendix 1 for the locality records of the 145 specimens examined.

### *Hyla pachyderma* Taylor

*Hyla pachyderma* Taylor, 1942d, p. 308 [holotype, U.S.N.M. No. 115029 from Pan de Olla, Veracruz, south of Tezuatlán, Puebla, México; Hobart M. Smith collector]. Smith and Taylor, 1948, p. 86. Duellman, 1964b, p. 485.

DIAGNOSIS: This small (snout-vent length in males, 39.9 mm.) member of the *Hyla bistincta* group has strong tarsal and thoracic folds, a bluntly round snout, vestigial web-

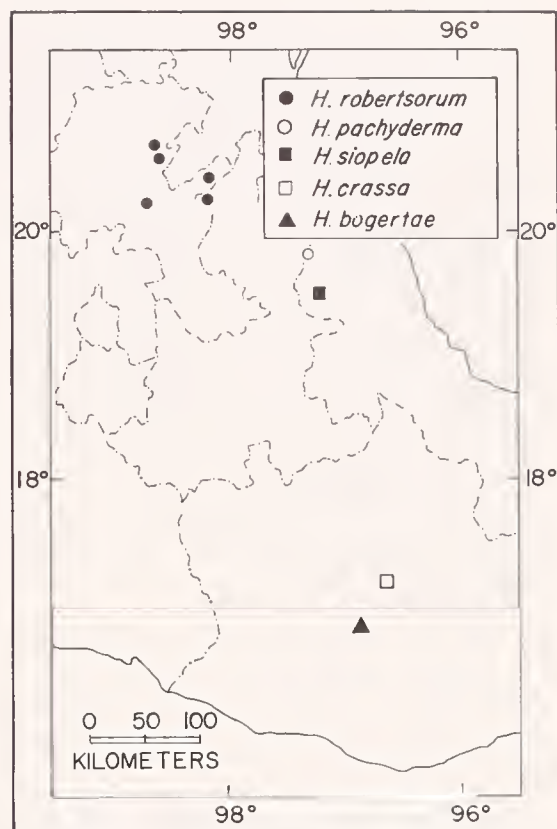


FIG. 241. Distribution of *Hyla robertsoni*, *pachyderma*, *siopela*, *crassa*, and *bogertae*.

bing between the fingers and moderately large nuptial spines on the prepollex in breeding males. The latter character is unique in the group and is present elsewhere in Middle American hylids only in *Hyla echinata* and in some species of *Ptychohyla*. *Hyla echinata* differs from *pachyderma* by having nearly fully webbed hands and dermal folds on the edges of the forearms and feet. Breeding males of the species of *Ptychohyla* have large ventrolateral glands, vocal slits, and short, webbed fingers.

DESCRIPTION: One male from Pan de Olla, Veracruz, México, has a snout-vent length of 39.9 mm.; the ratio of tibia length to snout-vent length is 0.526; the ratio of foot length to snout-vent length is 0.514; the ratio of head length to snout-vent length is 0.308, and the ratio of head width to snout-vent length is 0.321. The tympanum is not visible. Two females from the same locality have snout-

vent lengths of 52.7 to 55.7 (mean, 54.2) mm. The tympanum is visible in the females; the ratio of the diameter of the tympanum to that of the eye is 0.340 to 0.341 (mean, 0.341).

The head is slightly narrower than the body. The top of the head is flat; the eyes are large and prominent. In dorsal profile the snout is rounded; in lateral profile it is rounded above and truncate terminally. The snout is short; the nostrils are barely protuberant and situated about two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is barely concave, and the lips are thick, rounded, and not flared. A heavy dermal fold extends from the posterior corner of the eye to a point above the insertion of the arms. This fold completely obscures the upper part of the tympanum in all specimens; in the males the lower part of the tympanum is covered by thin skin so as not to be visible.

The arms are moderately short and robust; an axillary membrane is missing. A few small tubercles are present on the ventral surfaces of the forearms and a distinct dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are large and conical; they are present in a single row on the proximal segment of each digit. The palmar tubercle is low, flat and bifid. The prepollex is greatly enlarged; in a breeding male it bears a large clump of moderately large spines. The spines are present on the inner surfaces of the thumb and second finger. Only a vestige of webbing is present between the fingers (fig. 233D). The hind limbs are robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shanks. The tibiotarsal articulation extends to the anterior corner of the eye. A transverse dermal fold is present on the heel, and a thick low tarsal fold is present on the distal two-thirds of the tarsus. The inner metatarsal tubercle is moderately large, elliptical, and raised medially. The outer metatarsal tubercle is small and conical. The toes are long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately large and round, and the super-

numerary tubercles are distinct and subconical. The toes are about three-fourths webbed (fig. 235B). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the distal phalanx of the third, from the base of the fourth and on to the middle of the penultimate phalanx of the fifth.

The anal opening is directed posteroventrally at the midlevel of the thighs. A short anal sheath is present, and a distinct transverse dermal fold is present above the anal sheath. The skin on the dorsum and ventral surfaces of the limbs, except the thighs, is smooth; the skin on the chin, belly and ventral surfaces of the thighs is granular. A distinct thoracic fold is present. The tongue is ovoid, shallowly notched anteriorly and posteriorly and barely free behind. The dentigerous processes of the prevomers are small, ovoid, and situated in a transverse plane between the moderately large, nearly round choanae. One male has three teeth on each process for a total of six prevomerine teeth, whereas two females have four teeth on each process and a total of eight prevomerine teeth. Vocal slits and a vocal sac are absent.

No knowledge of the color of this species in life exists. In preservative the general coloration is dull grayish brown with indistinct, scattered, darker flecks on the dorsal surfaces (pl. 4, fig. 1). The flanks are grayish brown with cream reticulations, and the posterior surfaces of the thighs are tan. The chin is cream, mottled with brown. The belly is creamy yellow and is mottled with brown anteriorly in the females. A creamy white anal stripe is present, and in the females the stripe extends laterally in the form of a row of creamy white dashes and spots onto the posterodorsal surfaces of the thighs.

**TADPOLES:** No tadpoles of this species are known. Presumably they develop in mountain streams.

**MATING CALL:** The absence of vocal slits and a vocal sac precludes the presence of a call in this species.

**NATURAL HISTORY:** Taylor and Smith

(1945, p. 588) stated that the known specimens of *Hyla pachyderma* were found on bushes and weeds beside a small, bounding stream near Pan de Olla, Veracruz, México. I have searched unsuccessfully for this species in the area around Pan de Olla and Tezuatlán. Nothing more is known about the natural history of this species.

REMARKS: On the basis of the four specimens available for study, *Hyla pachyderma* seems to be closely related to *Hyla crassa* and *Hyla robertsoni*. Perhaps, these three species, as known now, are merely representatives of one taxon, but, if so, the differences between the known populations are distinctive. *Hyla pachyderma* is unique in the *Hyla bistincta* group by having moderately enlarged nuptial spines.

ETYMOLOGY: The specific name *pachyderma* is derived from the Greek, *pachys*, meaning thick, and the Greek *derma*, meaning skin; the name refers to the thick, glandular skin on the dorsum.

DISTRIBUTION: *Hyla pachyderma* is known only from a stream at an elevation of about 1600 meters on the Atlantic slopes of the Sierra Madre Oriental in central Veracruz, México (fig. 241).

See Appendix 1 for the locality records of the four specimens examined.

#### *Hyla siopela* Duellman

*Hyla siopela*, Duellman, 1968a, p. 570 [holotype, K.U. No. 100981 from the west slope of Cofre de Perote, Veracruz, México, elevation 2500-2550 meters; William E. Duellman collector].

DIAGNOSIS: This medium-sized (males attain snout-vent lengths of 46.2 mm.) member of the *Hyla bistincta* group lacks an axillary membrane, and vocal slits. It has webbing between the two outer fingers, and the toes are about two-thirds webbed. Small nuptial spines and a weak thoracic fold are present. The snout is truncate and has a weak, vertical rostral keel, a character not present in other members of the group. In northern Middle America the only other hylids with a rostral keel are some species of the genera *Ptychohyla* and *Plectrohyla*. In those species vocal slits are present; breeding males of *Ptychohyla* have spinous nuptial excrescences and ventrolateral glands, and males of *Plectrohyla* have projecting prepollical spines.

DESCRIPTION: *Hyla siopela* is a medium-sized species, in which the males attain a maximum snout-vent length of 46.2 mm., and females reach 52.5 mm. In a series of seven males from the Cofre de Perote, Veracruz, México, the snout-vent length is 42.1 to 46.2 (mean, 44.4) mm.; the ratio of the tibia length to snout-vent length is 0.472 to 0.500 (mean, 0.487); the ratio of foot length to snout-vent length is 0.456 to 0.495 (mean, 0.474); the ratio of head length to snout-vent length is 0.286 to 0.304 (mean, 0.296); the ratio of head width to snout-vent length is 0.291 to 0.317 (mean, 0.309), and the ratio of the diameter of the tympanum to that of the eye is 0.363 to 0.468 (mean, 0.438). Five females from the same locality have snout-vent lengths of 45.1 to 52.5 (mean, 49.6) mm. Females have noticeably larger tympani than do the males; the ratio of the diameter of the tympanum to that of the eyes in females is 0.500 to 0.545 (mean, 0.516).

The head is about as wide as the body; the top of the head is barely convex, and the eyes are large and prominent. In dorsal profile the snout is truncate with a faint, vertical rostral keel; in lateral profile the snout is truncate. The snout is short; the nostrils are protuberant and situated at about four-fifths of the distance from eyes to the tip of the snout. The canthus is angular; the loreal region is concave, and the lips are thick and not flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and thence downward to the point of insertion of the arm. The fold obscures the upper one-third of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is lacking. A row of small tubercles is present on the ventrolateral edge of the forearm, and a distinct dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs; that on the third finger is as large as the tympanum. The subarticular tubercles are moderately small and round; none is bifid. The supernumerary tubercles are small and in some specimens barely distinguishable; they are arranged in a single



row on the proximal segment of each digit. The palmar tubercle is low, flat, and barely visible. The prepollex is greatly enlarged and flattened ventrally. In breeding males it bears nuptial excrecence composed of minute horny spinules. The nuptial excrecence is also present on the inner surface of the thumb. Little webbing is present between the fingers (fig. 233E). The webbing is vestigial between the first and second fingers; the web extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the base of the penultimate phalanx of the fourth finger. The hind limbs are relatively short and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the posterior edge of the eye. A transverse dermal fold is present on the heel, and a thin tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, elongate, flat, and visible from above. The outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are moderately small and round; the supernumerary tubercles are small and arranged in a single row on the proximal segments of each digit. The toes are about two-thirds webbed (fig. 235C). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the midlevel of the thighs. A short anal sheath is present. The skin on the chin, belly, and posteroventral surfaces of the thighs is granular; elsewhere it is smooth. A weak thoracic fold is present. The tongue is broadly cordiform, notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are posteromedially inclined elevations between small ovoid choanae. Males have three to five teeth on each process

and a total of six to nine (mean, 7.9) prevomerine teeth. Females have four or five teeth on each process and a total of eight or nine (mean, 8.4) prevomerine teeth. A vocal sac and vocal slits are absent.

The general coloration of *Hyla siopela* is green or tan with darker reticulations (pl. 63, fig. 5). A typical adult male has a pale green dorsum with black spots and reticulations. The flanks are mottled dark brown and creamy white. The outer edges of the feet are silvery white with brown spots; the anterior and posterior surfaces of the thighs are dull brown, and the webbing and the first three toes are dull yellowish tan. The belly is creamy gray, and the throat is silvery white mottled with gray. The iris is dull bronze with black reticulations.

Some individuals have an olive-green or dark green dorsum with darker green or black flecks or reticulations; other individuals are pinkish tan or brown with dark brown flecks or reticulations. All specimens have some white markings above the anus and on the posterodorsal surfaces of the thighs; in some individuals the white flecks are expanded and interconnected to form an irregular white line.

In preservative the dorsum is dull grayish brown with small, irregularly shaped black spots on the head, back, and limbs. The flanks are gray mottled with creamy tan; the anterior and posterior surfaces of the thighs are tan. The belly is dull creamy tan, and the throat is marked with gray blotches. The anal region and posterior surfaces of the thighs are marked with small white spots. In most preserved specimens the dorsum is heavily marked with dark spots or flecks, but in some specimens relatively few dark flecks are present.

Juveniles have notably different coloration in life. The dorsum is uniformly pale green (pl. 63, fig. 4). The anterior and posterior surfaces of the thighs, fingers, first three toes and the webbing are deep yellow. The anal stripe is creamy white and the flanks are pale gray with black flecks. The upper lip, supratympanic fold, and canthal stripe are a bronze color. The belly is pale yellow with a silver cast on the throat. Juveniles having snout-vent lengths from 24.5 to 36.6 mm. are so col-



ored in life and are uniform dark bluish gray dorsally in preservative.

**TADPOLES:** Four specimens in advanced stages of development are available. Three specimens in developmental stage 41 have body lengths of 23 to 26 (mean, 24) mm. One specimen in developmental stage 37 has a body length of 26.5 mm. and a total length of 66.0 mm. The body is moderately depressed; the width is noticeably more than the depth. In dorsal profile the snout is bluntly rounded; in lateral profile the snout is inclined antero-ventrally from the nostril to a bluntly rounded tip. The nostrils are small, directed anteriorly, and situated slightly closer to the eyes than to the tip of the snout. The eyes are small, slightly elevated and directed dorsolaterally. The sinistral spiracle is short; the spiracular opening is directed posterodorsally at a point on the midline slightly less than half the distance from the snout to the posterior edge of the body. The anal tube is long and dextral. The tail is long, low, and bluntly rounded terminally. The caudal musculature is heavy and does not extend to the end of the caudal fin. At midlength of the tail, the depth of the musculature is equal to the depth of the ventral fin and is deeper than the depth of the dorsal fin. The dorsal fin does not extend onto the body (fig. 237D).

In preservative the body is dark grayish brown with bluish gray flecks ventrally. The tail is creamy tan with dark brown flecks. Only the periphery of the caudal fins is transparent.

The mouth is ventral and relatively small; its width is equal to about one-half of the greatest width of the body. The lateral folds in the lips are barely discernible. The mouth is completely bordered by two rows of small papillae; medial to these is an irregular row of larger papillae. The beaks are moderately slender and bear long, pointed serrations. The upper beak is in the form of a broad arch with short, blunt lateral processes. The lower beak also forms a broad arch. There are two upper and three lower rows of teeth. The upper rows are about equal in length, and the second upper row is narrowly interrupted medially. The lower rows are shorter than the upper ones and progressively shorter from the first to the third row (fig. 238D).

**MATING CALL:** The absence of vocal slits

and a vocal sac precludes the presence of a mating call in this species.

**NATURAL HISTORY:** This species inhabits relatively dry pine forests. All individuals were found along a stream, where both adults and juveniles were found in crevices and on rocks behind small cascading waterfalls by day or sitting on rocks or branches in the spray of cascades by night. Tadpoles were found in pools in the stream, where they hid under moss-covered banks.

**REMARKS:** MESSRS. Macreay J. Landy and John D. Lynch obtained the first specimens of this species on July 30-31, 1964. Their specimens were tentatively identified as *Hyla pachyderma*. I visited the stream on Cofre de Perote in February, 1966; at that time, no frogs were found. Mr. Howard L. Freeman visited the locality on June 18, 1966, and obtained several frogs and four tadpoles. I returned to the stream on July 30, 1966, and obtained several frogs, but no tadpoles. The examination of the fresh material and comparison of it with the specimens obtained by Landy and Lynch and with the type series of *Hyla pachyderma* led to the conclusion that the frogs inhabiting Cofre de Perote represented a distinct and previously unnamed species (Duellman, 1968a, p. 570).

**ETYMOLOGY:** The specific name is derived from the Greek *siopelos*, meaning silent, and is used in allusion to the absence of a voice in the species.

**DISTRIBUTION:** *Hyla siopela* is known only from a small stream on the west slope of Cofre de Perote, in the Sierra Madre Oriental in central Veracruz, México, at an elevation of 2500 to 2550 meters (fig. 241).

See Appendix 1 for the locality records of the 54 specimens examined.

### *Hyla crassa* (Brocchi)

*Cauphias crassus* Brocchi, 1877b, p. 130 [holotype, M.N.H.N. No. 6331 from "México"; Adolpe Boucard collector].

*Cauphias crassum* Brocchi, 1882a, p. 64. Kellogg, 1932, p. 118.

*Hyla crassa*: Boulenger, 1882a, p. 396. Günther, 1901 (1885-1902), p. 281. Smith and Taylor, 1948, p. 86. Duellman, 1964b, p. 486.

*Hyssiboas crassus*: Cope, 1887, p. 14.

*Hyla robustofemora* Taylor, 1940c, p. 239 [holotype, U.I.M.N.H. No. 25050 (formerly E.H.T.-H.M.S.)

No. 16314) from Cerro San Felipe, 15 kilometers northeast of Oaxaca de Juárez, Oaxaca, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 86.

*Plectrohyla crassa*: Hartweg, 1941, p. 1.

**DIAGNOSIS:** This large (males attain a length of 53.7 mm.) member of the *Hyla bistincta* group has a strong tarsal fold, small nuptial spines, a round snout, and vestigial webbing on the hand. Vocal slits, axillary membranes, and a thoracic fold are absent. The feet are webbed to the base of the discs. By this character alone *crassa* can be distinguished from all other members of the *Hyla bistincta* group.

**DESCRIPTION:** One adult male from Cerro San Felipe, Oaxaca, México, has a snout-vent length of 53.7 mm.; the ratio of tibia length to snout-vent length is 0.501; the ratio of foot length to snout-vent length is 0.473; the ratio of head length to snout-vent length is 0.298; the ratio of head width to snout-vent length is 0.328, and the ratio of the diameter of the tympanum to that of the eye is 0.278. A female from an unknown locality has a snout-vent length of 48.2 mm. In the female, the tympanum is completely concealed; otherwise, it resembles the male in proportions.

The head is slightly narrower than the body and barely convex on top. In dorsal profile, the snout is broadly rounded and in lateral profile, bluntly rounded. The snout is short; the nostrils are barely protuberant and are situated about two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is barely concave, and the lips are thick and not flared. A heavy dermal fold extends posteroventrally from the posterior corner of the eye to a point above the insertion of the arm; this fold obscures the entire tympanum in one female and the upper half of the tympanum in the one male. Otherwise, the tympanum is barely discernible and is separated from the eye by a distance half again the length of the diameter of the tympanum.

The arms are short and thick; no axillary membrane is present. Tubercles are absent along the ventrolateral edge of the forearm, but a distinct dermal fold is present on the wrist. The fingers are moderately long and slender and bear moderately large discs; the disc on the third finger is somewhat larger

than the diameter of the tympanum. The subarticular tubercles are moderately small and round; none is bifid. The supernumerary tubercles are large and subconical. The palmar tubercle is large, flat, and partially bifid. The prepollex is greatly enlarged and rounded; in the one male it bears a nuptial excrescence composed of minute spinules. The nuptial excrescence also is present on the penultimate phalanges of the first and second fingers. The fingers essentially lack webbing (fig. 233F). There is no web between the first and second fingers and only rudimentary web between the others. The hind limbs are short and robust; the heels of the adpressed limbs overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A transverse dermal fold is present on the heel, and a thick tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is rather small, ovoid, and rounded. The outer metatarsal tubercle is small, flat, and indistinct. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately large and round; the supernumerary tubercles are large, low, and arranged in a single row on the proximal segments of each digit. The toes are fully webbed (fig. 235D). A dermal fringe is present on the inner edge of the first toe and the outer edge of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs; an elongate anal sheath is present, and small tubercles are present below the anal opening. The skin on the dorsal surface of the body is smooth, but it is somewhat granular on the dorsal surfaces of the limbs. The skin on the chin and belly is moderately granular, and that on the ventral surfaces of the thighs is heavily granular. There is no thoracic fold. The tongue is nearly round, shallowly notched posteriorly and free behind for about one-fourth of its length. The denticulous processes of the prevomers are elliptical in shape and situated on a transverse plane between the small ovoid choanae. One male has five teeth on each process, and one female has seven and eight teeth on each process. Vocal slits and the vocal sac are absent.

The general coloration of this frog in preservative is dull brown (pl. 4, fig. 2). The venter is dull creamy tan with brown suffusion on the throat and ventral surfaces of the hind limbs. A few creamy yellow spots are present on the flanks.

Taylor (1940c, p. 392), in his description of *Hyla robustofemora*, stated: "Above, a uniform dull olive-green, somewhat lighter on the sides of the head and body; chin, gray with yellow flecks; abdomen, creamy yellow with some pigmentation posteriorly, especially under posterior part of femur; palms and soles, dark lavender-gray; posterior side of femur gray with wash of yellow; a cream spot under forearm; a few cream spots on side, on anterior face of femur, and at knee and heel; a dim spot of cream on anal flap."

The only other known specimen, a female (M.N.H.N. No. 6331, the holotype of *Hyla crassa*) has more cream mottling on the flanks and posterior surfaces of the thighs and more distinct mottling on the throat than does the male; these differences were used as the basis of description of *Hyla robustofemora*.

**TADPOLES:** No tadpoles of this species have been found.

**MATING CALL:** The absence of vocal slits and a vocal sac preclude the presence of a call in this species.

**NATURAL HISTORY:** The only knowledge of the natural history of this species is incorporated in a brief statement by Taylor (1940c, p. 389): "In the summer of 1938, I obtained a specimen of an undescribed *Hyla* at night, hopping along the edge of a small spring-fed rivulet at an elevation of about 2300 meters on the Cerro San Felipe. The frog, frightened by my approach, jumped into the rivulet, swam to the opposite side and clamored up the bank, without attempting to hide under the water."

**REMARKS:** The systematic status of *Caulophias crassus* Brocchi remained in doubt from the time of its original description until Duellman (1964b, p. 488) re-examined the type specimen and compared it with the holotype of *Hyla robustofemora* (U.I.M.N.H. No. 25050). Brocchi (1877b, p. 130) and Kellogg (1932, p. 118) erroneously stated that the terminal phalanges in the holotype of *Caulophias crassus* were T-shaped and that the

terminal phalanx was not preceded by an intercalary cartilage. Duellman (1964b, p. 489) stated: "The type of *Caulophias crassus* possesses intercalary cartilages between the penultimate and terminal phalanges; the latter are not T-shaped, but as in the type of *Hyla robustofemora* resemble those typical of *Hyla*."

**ETYMOLOGY:** The specific name is derived from the Latin *crassus*, meaning thick or fat and alludes to the robust appearance.

**DISTRIBUTION:** *Hyla crassa* is known only from a small stream at an elevation of 2300 meters in the mountains of central Oaxaca, México (fig. 241).<sup>14</sup>

See Appendix 1 for the locality records of the two specimens examined.

### *Hyla bogertae* Straughan and Wright

*Hyla bogertae* Straughan and Wright, 1969, p. 1 [holotype, L.A.C.M. No. 44400 from a tributary of the Río Atoyac, below Vivero El Tapanal, 1.6 kilometers south of La Cofradia, Distrito Sola de Vega, Oaxaca, México, elevation 2652 meters; Ian R. Straughan and John W. Wright collectors].

**DIAGNOSIS:** *Hyla bogertae* is a moderately large (snout-vent length in one adult male, 45.1 mm.) member of the *Hyla bistincta* group with a rounded snout, discontinuous tarsal fold, and non-spinous nuptial pads in breeding males. Vocal slits, axillary membranes, thoracic fold, and webbing on the hand are absent. *Hyla bogertae* is similar to *robertsorum*, which has vestigial webbing between the fingers and a weak thoracic fold; furthermore, there are differences in coloration: *robertsorum* has dark brown flanks with small cream spots and a gray belly, whereas *bogertae* has olive-green flanks with large yellow spots and a white belly. *Hyla siopela* differs from *bogertae* by having a more truncate snout with a weak rostral keel and less webbing (2/3 in *siopela*; 4/5 in *bogertae*). *Hyla pachyderma* differs from *bogertae* by having a strong thoracic fold and large nup-

<sup>14</sup> In April, 1969, Mr. Chuck McClung collected five specimens of this species from rock crevices at a locality 14.4 kilometers northeast of Ciudad Oaxaca, Oaxaca. I have no further details concerning the locality but suspect that it is in the highland mass associated with Cerro San Felipe. Three specimens are preserved in the United States National Museum, and one is in the Museum of Natural History at the University of Kansas.



tial spines in breeding males. *Hyla crassa* differs by having the feet fully webbed and a strong tarsal fold. *Hyla bistincta* and *pentheter* differ from *bogertae* by having a strong tarsal fold and an elongate anal sheath (short in *bogertae*).

**DESCRIPTION:** The one adult male has a snout-vent length of 45.1 mm.; three adult females have snout-vent lengths of 43.3 to 50.1 (mean, 47.6) mm. In the one male the ratio of tibia length to snout-vent length is 0.505; the ratio of head length to snout-vent length is 0.262; the ratio of head width to snout-vent length is 0.365; and the ratio of the diameter of the tympanum to that of the eye is 0.404. The proportions of the three females are about the same as those of the male, except that the tympanum is proportionately smaller to the eye in the females; the ratio of the diameter of the tympanum to that of the eye is 0.333 to 0.400 (mean, 0.371).

The head is slightly narrower than the body; the top of the head is barely convex. In dorsal profile the snout is bluntly rounded; in lateral profile, the snout is truncate and rounded above. The snout is short; the nostrils are slightly protuberant and situated about three-fourths of the distance from the eyes to the tip of the snout; the internarial region is slightly depressed. The canthus is rounded; the loreal region is concave, and the lips are thick and rounded. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and angles downward to a point above the insertion of the arm. The fold covers the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is absent. A few small tubercles are present on the ventrolateral edge of the forearm, and a weak dermal fold is present or absent on the wrist. The fingers are long and slender and bear small discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are moderately large and low; they are arranged in a single row on the proximal segment of each digit. The outer palmar tubercle is low,

rounded, and bifid. The prepollex is enlarged and rounded. A horny nuptial excrecence is present in the one breeding male. Webbing is absent between the fingers. The hind limbs are robust; the heels of the adpressed limbs barely overlap. A heavy transverse dermal fold is present on the heel. The tarsal fold is interrupted and essentially consists of a series of low tubercles. The inner metatarsal tubercle is small and ovoid; the outer metatarsal tubercle is small and subconical. The toes are moderately long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are large and round. The supernumerary tubercles are small and present in a single row. The toes are about four-fifths webbed; the webbing extends to the base of the discs on all toes, except the fourth, where it extends to the base of the penultimate phalanx.

The anal opening is directed posteroventrally near the midlevel of the thighs; it is covered by a short anal sheath. The skin on the dorsum and ventral surfaces of the arms, shanks, and feet is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. A thoracic fold is lacking. The tongue is broadly cordiform, barely notched behind, and free posteriorly for about one-fourth of its length. The prevomerine teeth are situated on posteromedially inclined elevations between the small, ovoid choanae. In one female there are nine prevomerine teeth, and in one male there are six teeth. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla bogertae* is dark brown with indistinct tan spots dorsally. The brown gives way to gray laterally with gray and white spots on the flanks and lips. The dorsal surfaces of the limbs are mottled brown and gray. The posterior surfaces of the thighs are dark brown. A white anal stripe is present. The throat is dark brown with cream spots. The rest of the ventral surfaces are uniform creamy white, except the hands and feet, which are dark brown.

Straughan and Wright (1969, p. 3) described the coloration in life of the female holotype: "Dorsal surface of body and limbs olive green (gun metal gray in alcohol) with extensive silver to pale bronze reticulation,



largely maintained in alcohol. Light bar above level of cloaca at beginning of ventral granularity. Ventral surface of body white with yellow wash along flanks. Limbs mainly darker with yellow in groin area, around heels, upper arm, and elbow. Throat darker olive with large yellow spots and minute creamy pustules." Straughan and Wright (1969, p. 6) noted the coloration of the male allotype: "Color darker than in holotype with essentially the same pattern, but slightly less development; throat color darker and more extensive than in holotype. In all other characters allotype agrees with holotype."

**TADPOLES:** Three tadpoles in developmental stage 25 have total lengths of 30 to 32 mm., and four in developmental stage 30 have total lengths of 52 to 57 mm. A typical tadpole in developmental stage 30 has a body length of 19.1 mm. and a total length of 55.7 mm. The body is depressed and slightly wider than deep. In dorsal and lateral profiles the snout is bluntly rounded. The nostrils are small, directed anterolaterally, and situated about midway between the eyes and the tip of the snout. The eyes are moderately small and directed dorsolaterally. The spiracle is sinistral; its opening is directed posteriorly at a point on the midline at about midlength of the body. The cloacal tube is moderately long and dextral. The tail is long, low, and terminally rounded. The caudal musculature is robust and moderately deep; at midlength of the tail the depth of the caudal musculature is only slightly less than the depth of the dorsal fin, which does not extend onto the body.

The body is dark grayish brown dorsally and slightly paler laterally with scattered black flecks and golden lichenous markings. The caudal musculature is tan, and the fins are translucent tan. Dark brown spots are scattered on the caudal musculature and fins.

The mouth is ventral and moderately large; its width is equal to about two-thirds of the width of the body. Lateral folds are present in the lips, which are bordered by two rows of small papillae. Median to the small labial papillae there is one row of larger papillae on the upper lip and two rows on the lower lip. A few large papillae are present in the lateral folds. The beaks are

moderately robust and bear small serrations. The upper beak is in the form of a broad arch with long, rather slender, terminally rounded lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are about equal in length and slightly longer than the lower rows. The second upper row is narrowly interrupted medially.

Tadpoles in developmental stage 25 have dark spots on the caudal musculature and dorsal fin but lack spots on the ventral fin. These tadpoles also have a proportionately shorter tail than do tadpoles in stage 30.

**MATING CALL:** The apparent absence of vocal slits and a vocal sac preclude the presence of a mating call in this subspecies.

**NATURAL HISTORY:** The only information on the habits and habitat of this species was given by Straughan and Wright (1969, p. 8): "All individuals were collected from a system of small and medium sized streams flowing down steep slopes in pine-fir forest. Adults and juveniles were encountered sitting on rocks or piles of detritus deposited by flood. The main stream consisted of small pools (two to three m wide) with sandy bottoms partially covered with leaf litter, and small water falls and rapids (one-half to one and one-half m wide). When disturbed, the frogs jumped into the water and remained submerged for a short period before re-emerging. Water temperature at time of capture of frogs was 14° C. Tadpoles were found in the larger pools resting on the bottom in quieter water."

Straughan and Wright (1969, p. 8) metamorphosed one tadpole in the laboratory. At metamorphosis the young frog had a snout-vent length of 20.2 mm.

**REMARKS:** This species was described after the manuscript for the present publication was completed. Subsequently I examined the known specimens and included data on the species in the text; however, because the illustrations had been mounted and arranged, I was not able to insert illustrations of this species. The reader is referred to the type description (Straughan and Wright, 1969) for photographs of adults and young and drawings of tadpoles and the mouth of a tadpole.

I concur with Straughan and Wright (1969, p. 8) that *Hyla bogertae* is related to

the high montane complex of species containing *crassa*, *pachyderma*, *robertsoni*, and *siopela*. Until osteological data are available for all of those species, no further comments on relationships can be justified.

**ETYMOLOGY:** The specific name is a patronym for Martha M. Bogert.

**DISTRIBUTION:** *Hyla bogertae* is known only from one small stream system at an elevation of 2652 meters in the Sierra Madre del Sur in Oaxaca, México.

See Appendix 1 for the locality records of the 15 specimens examined.

### The *Hyla eximia* Group

**DEFINITION:** The members of this group are moderate-sized species; males attain a maximum snout-vent length of 44 mm., and females 47 mm. The dorsum in most species is green, with or without brown spots or stripes, but in some the dorsum is tan or gray with darker spots. A dark face mask is present (except in *cadaverina*), and the posterior surfaces of the thighs are uniformly colored (pale yellow spots in *euphorbiacea*). The palpebral membrane is clear. The fingers have vestigial webbing, and the hands are no more than two-thirds webbed. Dermal fringes and appendages are absent on the limbs. A tarsal fold is present, but an axillary membrane is lacking. Males have single, median, subgular vocal sacs and usually have small, horny, nuptial excreseences on the thumbs. The cranial elements are weakly ossified, and a large frontoparietal fontanelle is present (fig. 242). The nasals are moderately small and not in bony contact with the sphenethmoid, which is not ossified anteriorly between the nasals. The quadratojugal is present and in contact with the maxillary. The squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends only about one-third of the distance to the maxillary. The columella is expanded distally. The prevomers are poorly ossified and bear teeth. The palatine is weak, and the medial ramus of the pterygoid does not articulate with the prootic. The tadpoles have deep fins and small anteroventral mouths with two upper and three lower rows of teeth. The mating calls consist of a series of short notes or a series of rattling notes. The haploid number of chromosomes is 12.

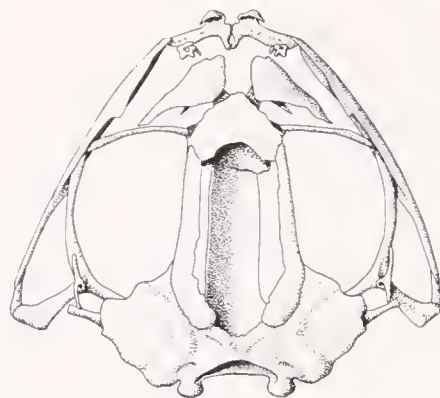


FIG. 242. Dorsal view of the skull of *Hyla eximia*, K.U. No. 59903.  $\times 6$ .

**COMPOSITION:** Seven species comprise the group, which is widespread in North America. One species, *Hyla squirella* of southeastern group, which is widespread in North America. all of the others occur in México, although the greatest part of the range of *Hyla regilla* is in the United States. Of the six species occurring in Middle America, 3843 preserved frogs, 22 skeletons, 15 lots of tadpoles, and one clutch of eggs have been examined from México and Guatemala. Additional material, principally skeletons and tadpoles, has been examined from the United States.

**COMMENTS:** The arrangement of species used here differs notably from that presented by earlier workers. Taylor (1939b) first recognized an *eximia* group, in which he placed *lafrentzi*, *regilla*, *euphorbiacea*, and *eximia*; he named two other species (*cardenasi* and *wrightorum*) in the same group. Taylor concluded that *Hyla bocourti* was a synonym of *euphorbiacea* and that *Hyla gracilipes* was a synonym of *eximia*. Taylor (1941) named *Hyla arboricola*, an *eximia*-like frog from the Sierra Madre del Sur in Guerrero. Stuart (1954b) named *Hyla walkeri* from Guatemala; he suggested that *walkeri* was most like *arboricola*. Maslin (1957) named *Hyla microeximia* from Jalisco, but Duellman (1961e) showed that Maslin's species was based only on a common pattern of *eximia*. Thus, for about two decades the *eximia* group remained only a simple assortment of nondescript tree frogs that inhabited the highlands of western North America southward to Guatemala. Then, seemingly as though by explosive evo-

lution the complexities of the group multiplied. Blair (1960) and Bogert (1960) pointed out the apparent mosaic of call-types in *eximia* on the Mexican plateau. Gorman (1960) showed that the populations of "*Hyla arenicolor*" west of the Colorado Desert were not really *arenicolor* but represented a distinct species, which he named *californiae* and placed in the *eximia* group.

Blair (1960) added *Hyla squirella* to the *eximia* group. The structure of the adult and tadpole, the life history, and the mating call seem to ally this vicariant species with the *eximia* group. However, Blair's suggestion that *Hyla staufferi* be placed in the *eximia* group is as preposterous as Kellogg's (1932) inclusion of *Hyla smithii* as a synonym of *eximia*. Blair's idea of the relationships of *staufferi* was based entirely on similarities in the mating call of *staufferi* and *eximia* and without regard to morphology and distribution.

Jameson, Mackey, and Richmond (1966) presented the most diverse arrangement yet of the *eximia* group. On the basis of a multivariate discriminant analysis of 10 measurements of each of 454 specimens they recognized ten subspecies of *Hyla regilla*, including *lafrentzi* and *wrightorum*. Thus, where Taylor in 1939 recognized six taxa, 18 exist today. Most of the races of *Hyla regilla* do not occur in México and consequently will not be dealt with here. In order that the recognizable populations can be discussed here, the taxonomic status of the various nominate species and subspecies is outlined below. Each is elaborated upon more fully in the accounts of the appropriate species.

*Hyla eximia* possibly is a composite species comprised of two or more populations not, or but little, differentiated morphologically. This possibility notwithstanding, several named species (*gracilipes*, *cardenasi*, *wrightorum*, *arboricola*, and *microeximia*) are considered to be synonyms; all were distinguished from *eximia* by minor morphological characters. The northern populations formerly assigned to *wrightorum* are not conspecific with *Hyla regilla*.

*Hyla euphorbiacea* includes *Hyla bocourti* and is specifically distinct from *eximia*. *Hyla walkeri* is a distinct vicariant most closely related to *euphorbiacea*.

*Hyla plicata* is an earlier name for *Hyla lafrentzi*, a species distinct from *regilla* and occurring in partial sympatry with *eximia*.

The Mexican populations of *Hyla regilla* can be assigned to two subspecies; those to the south of the Viscaíno Desert are *H. r. curta*, and those to the north of the desert are considered to be representatives of *H. r. hypochondriaca* (*deserticola* is a synonym).

The frogs named *Hyla californiae* by Gorman (1960) were originally named *Hyla nebulosa* by Hallowell (1854). Cope (1866a) pointed out that Hallowell's name was preoccupied and proposed the replacement name *Hyla cadaverina*, which is the correct name for the species that for so many years masqueraded under the name *Hyla arenicolor* and for less than a decade enjoyed specific recognition under a junior objective synonym (Duellman, 1968c).

The definition and recognition of species in the *eximia* group is difficult due to subtle differences that are inconspicuous in light of gross similarities and to the absence of easily definable characters in the preserved frogs. In this respect, the species in the *eximia* group are like those in the *Hyla microcephala* group. Osteological differences among the species are lacking or insignificant. The rugose dorsal skin immediately distinguishes *cadaverina* and *regilla* from the other species in the group. Some slight variation in the structure of the hands and feet and in the amount of webbing is evident (figs. 243 and 244). Differences in coloration are useful specific characters but do not tend to elucidate interspecific relationships. *Hyla euphorbiacea* is distinctive by having yellow spots on the posterior surfaces of the thighs, and *plicata* has a white stripe on the shank; these are the only distinctive color differences in the smooth-skinned species. Slight differences in size and proportions are evident (table 45). *Hyla plicata* is the largest species and has the longest legs. *Hyla regilla* and *cadaverina* have proportionately larger heads and smaller tympani than the other species. These differences, except for the large size and long legs of *plicata*, are negated in *eximia* by the extreme variation in that species (see account of *Hyla eximia* for details of variation). The differences in the tadpoles are very slight, except for those of





FIG. 243. Hands of members of the *Hyla eximia* group. A. *Hyla regilla*, K.U. No. 109875. B. *Hyla cadaverina*, K.U. No. 109866. C. *Hyla eximia*, U.M.M.Z. No. 119163. D. *Hyla euphorbiacea*, K.U. No. 100924. E. *Hyla walkeri*, K.U. No. 57835. F. *Hyla plicata*, K.U. No. 57384.  $\times 5$ .

*cadaverina* and *regilla* (figs. 245 and 246); unfortunately, the tadpole of *plicata* is unknown.

The mating calls offer some excellent clues to the relationships of the species (table 46; pls. 12-14). The calls of *euphorbiacea* and *walkeri* consist of groups of quickly repeated short notes, whereas the calls of the other species are made up of equally dispersed notes. The notes produced by *plicata* are longer and have a lower dominant frequency than those of the other species. The mating calls of members of sympatric pairs of species (*eximia-plicata* and *cadaverina-regilla*)

differ in several parameters and doubtlessly act as important reproductive isolating mechanisms.

The relationships of the *eximia* group seem to be with the *Hyla cinerea* group and with *Pseudacris* in North America.

#### ***Hyla regilla* Baird and Girard**

*Hyla regilla* Baird and Girard, 1852, p. 174.

**DIAGNOSIS:** This moderately small species has small discs, little or no webbing between the fingers, and the toes about two-thirds webbed. The dorsal ground color is green, gray, tan, brown, or reddish brown, and the



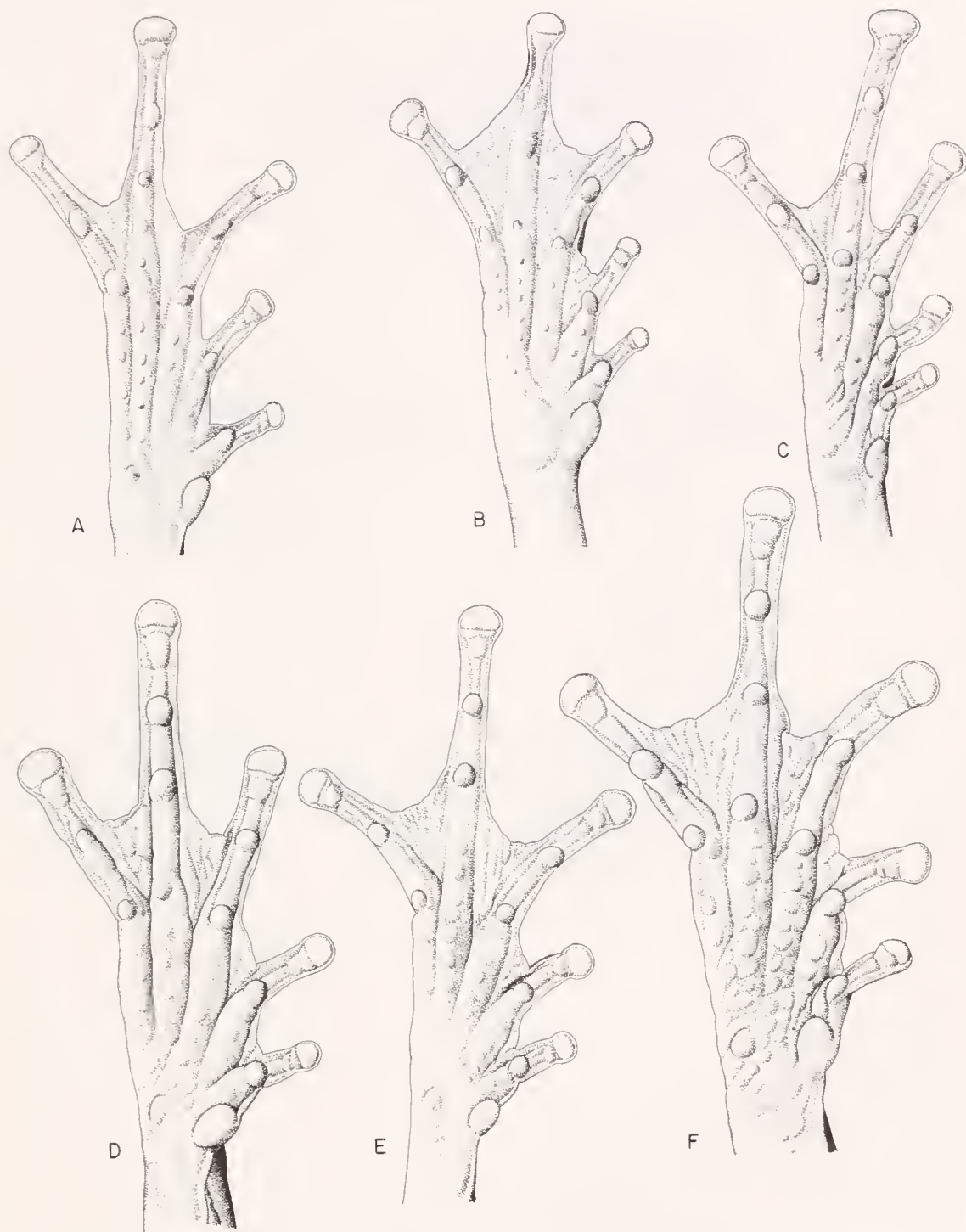


FIG. 244. Feet of members of the *Hyla eximia* group. A. *Hyla regilla*, K.U. No. 109875. B. *Hyla cada-verina*, K.U. No. 109866. C. *Hyla eximia*, U.M.M.Z. No. 119163. D. *Hyla euphorbiacea*, K.U. No. 100924. E. *Hyla walkeri*, K.U. No. 57835. F. *Hyla plicata*, K.U. No. 57384.  $\times 5$ .

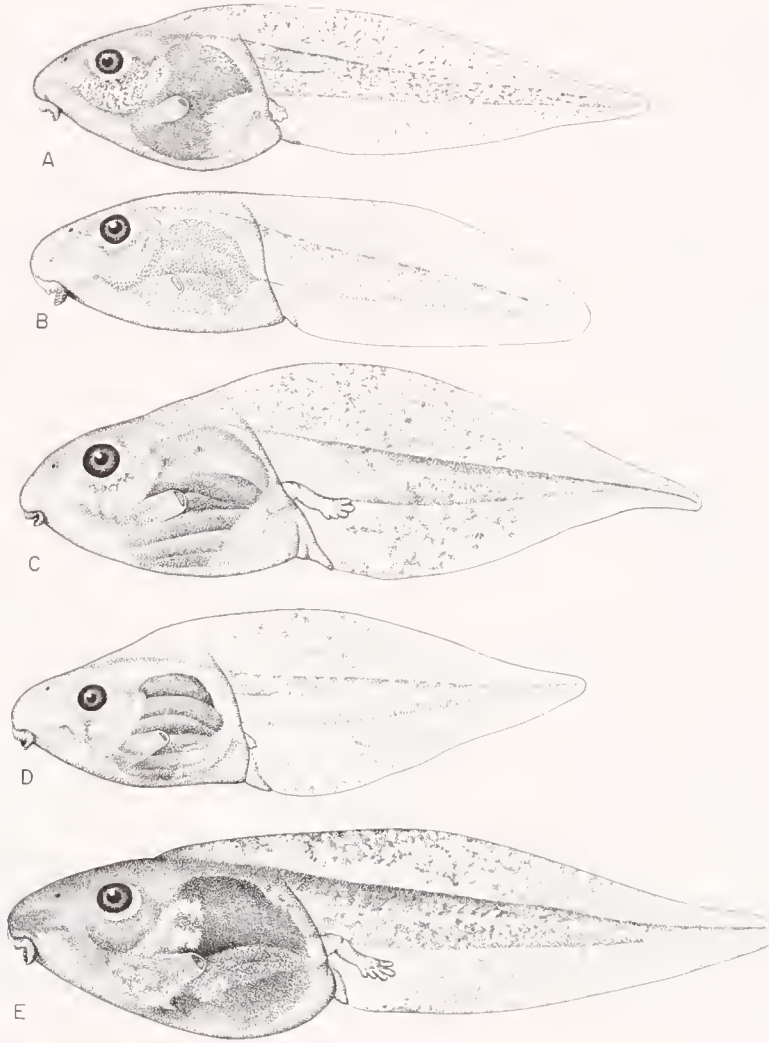


FIG. 245. Tadpoles of members of the *Hyla eximia* group. A. *Hyla regilla*, K.U. No. 118150. B. *Hyla cadaverina*, K.U. No. 118149. C. *Hyla eximia*, K.U. No. 104133. D. *Hyla euphorbiacea*, K.U. No. 59988. E. *Hyla walkeri*, K.U. No. 60003.  $\times 3$ .

dorsum usually is marked with dark brown longitudinal dashes or irregular stripes. A dark brown face mask is always present, and a dark interorbital triangular mark usually is present. Dark brown spots or flecks are present on the flanks, and dark transverse bars are evident on the dorsal surfaces of the thighs. The skin of the dorsum is smooth or weakly pustulate; *Hyla cadaverina* has tuberculate skin, the toes three-fourths webbed, and no dark face mask. Other members of the *Hyla eximia* group have a green dorsal

ground color but lack an interorbital triangular mark. Three other small Mexican hylids have an interorbital triangular mark; of these *Acris crepitans* has a pointed snout, tuberculate dorsum, and fully webbed feet. *Pseudacris clarkii* has a pointed snout and the toes no more than one-third webbed, and *Hyla staufferi* has a protruding acuminate snout and much larger discs.

CONTENT: In the most recent review of this species, Jameson, Maekey, and Richmond (1966) recognized ten subspecies of *Hyla*

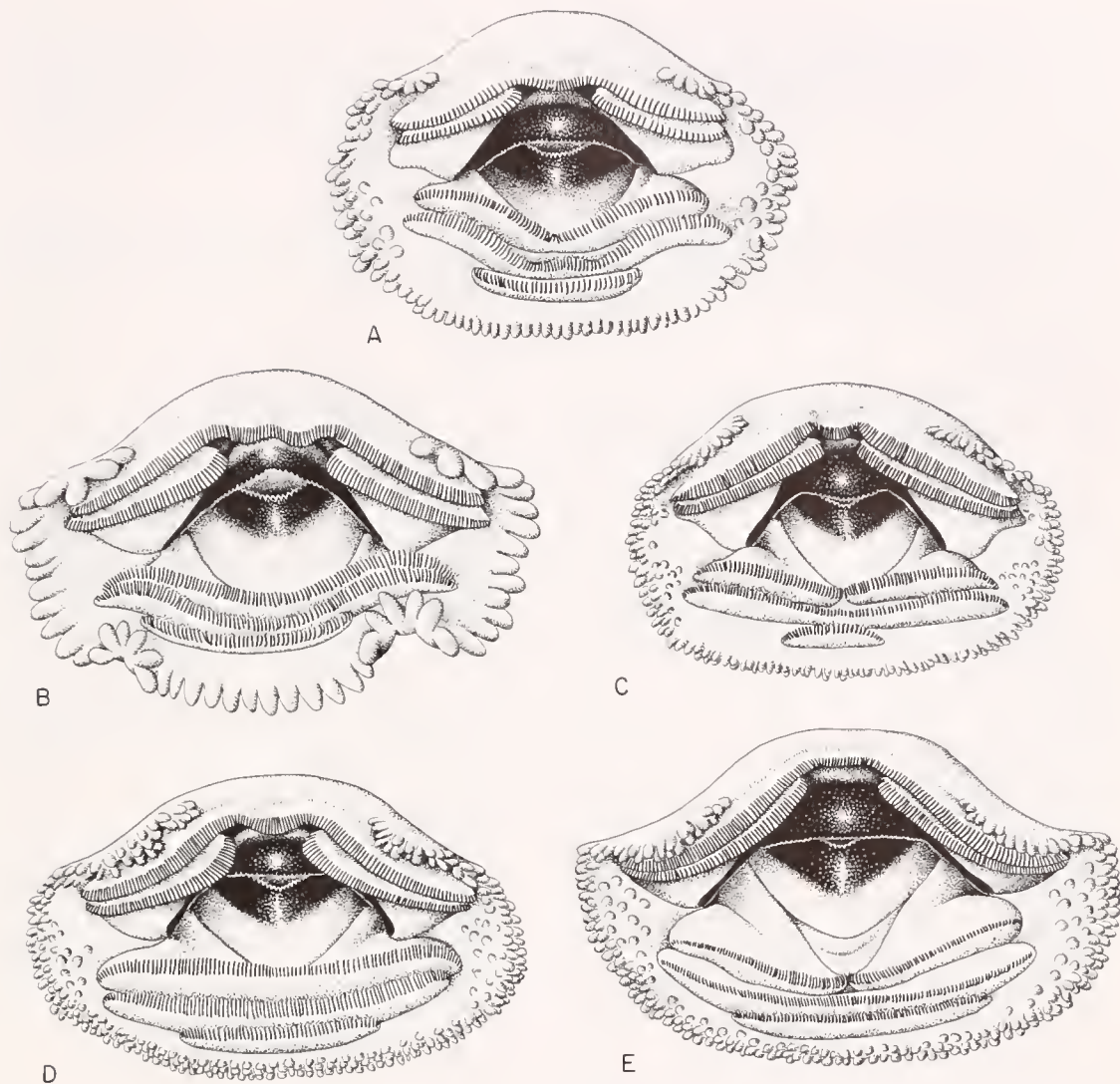


FIG. 246. Mouths of tadpoles of members of the *Hyla eximia* group. A. *Hyla regilla*, K.U. No. 118150. B. *Hyla cadaverina*, K.U. No. 118149. C. *Hyla eximia*, K.U. No. 104133. D. *Hyla euphorbiacea*, K.U. No. 59988. E. *Hyla walkeri*, K.U. No. 60003.  $\times 30$ .

*regilla*. Duellman (1968c) showed that *Hyla regilla lafrentzi* (= *Hyla plicata*) was specifically distinct from *regilla*. I here conclude that *Hyla regilla wrightorum* is indistinguishable from *eximia* but consider *eximia* to be specifically distinct from *regilla*. Furthermore, I consider *Hyla regilla deserticola* and *hypochondriaca* to be the same. According to this arrangement, seven subspecies are recognized; five of these occur only to the north of México and have not been studied by me. The

Mexican populations are assignable to *Hyla regilla curta* and *H. r. hypochondriaca*.

DISTRIBUTION: *Hyla regilla* ranges from sea level to elevations of about 3400 meters from southern British Columbia, Canada, southward through the mountains and along the coastal regions of western United States to the southern tip of the peninsula of Baja California, México, and eastward to western Montana and Idaho and eastern Nevada in the United States (fig. 247).



TABLE 45  
Comparison of Sizes and Proportions, with Means in Parentheses, of Males  
of Species in the *Hyla eximia* Group.

Species	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
<i>H. regilla</i> .....	36	26.6-37.8 (31.9)	0.438-0.502 (0.476)	0.413-0.498 (0.453)	0.312-0.350 (0.329)	0.326-0.378 (0.354)	0.344-0.625 (0.499)
<i>H. cadaverina</i> .....	21	26.0-35.9 (32.3)	0.467-0.534 (0.499)	0.412-0.477 (0.441)	0.334-0.383 (0.354)	0.383-0.417 (0.399)	0.421-0.545 (0.479)
<i>H. plicata</i> .....	41	34.5-41.6 (37.9)	0.464-0.570 (0.509)	0.449-0.539 (0.486)	0.291-0.324 (0.309)	0.334-0.420 (0.367)	0.421-0.650 (0.523)
<i>H. eximia</i> .....	120	24.6-34.9 (29.7)	0.427-0.524 (0.470)	0.415-0.504 (0.461)	0.274-0.346 (0.302)	0.296-0.367 (0.335)	0.474-0.692 (0.563)
<i>H. euphorbiacea</i> .....	50	31.6-39.6 (35.7)	0.434-0.497 (0.460)	0.410-0.490 (0.448)	0.270-0.323 (0.296)	0.304-0.365 (0.339)	0.462-0.710 (0.599)
<i>H. walkeri</i> .....	60	26.4-35.9 (32.2)	0.425-0.514 (0.476)	0.408-0.494 (0.459)	0.270-0.324 (0.309)	0.308-0.362 (0.337)	0.433-0.633 (0.523)

TABLE 46  
Comparison of Mating Calls, with Means in Parentheses, of the Species in the *Hyla eximia* Group.

Species	N	Notes per Call Group	Group Repetition Rate (min.)	Note Repetition Rate (min.)	Duration of Notes (sec.)	Pulse Rate (per sec.)	Fundamental Frequencies (cps) Dominant
<i>H. regilla curta</i> .....	1	1	---	30	0.10	---	2420
<i>H. cadaverina</i> .....	4	1	---	44-50 (47)	0.12-0.15 (0.135)	125-135 (131)	2055-2080 (2073)
<i>H. plicata</i> .....	3	1	---	24-60 (40)	0.52-0.72 (0.630)	78-98 (90)	1328-1632 (1495)
<i>H. eximia</i> .....	34	1	---	40-156 (76)	0.15-0.42 (0.227)	48-130 (81.7)	1740-2704 (2058)
<i>H. euphorbiacea</i> .....	23	5-10	12-39	300-935 (664)	0.04-0.11 (0.06)	65-120 (103)	1653-2782 (2168)
<i>H. walkeri</i> .....	4	4-6	30-48	960-1200 (1090)	0.03-0.04 (0.035)	120 (158)	1755-2175 (1910)

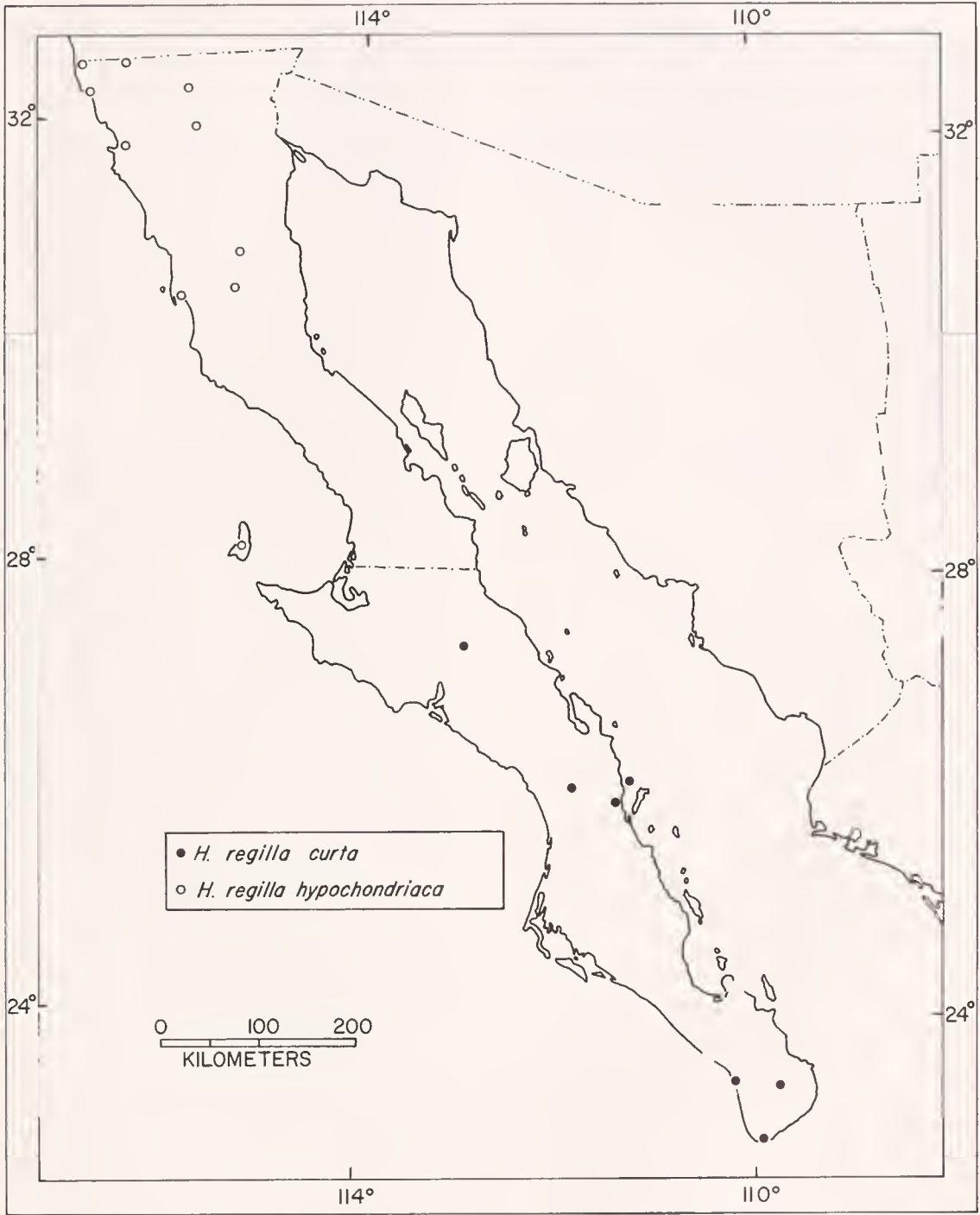


FIG. 247. Distribution of the subspecies of *Hyla regilla* in México.

*Hyla regilla curta* Cope

*Hyla curta* Cope, 1887b, p. 313 [syntypes, U.S.N.M. No. 5293 (19 specimens) from Soria, 15 miles north of Cabo San Lucas, Baja California Sur, México; John Xanthus collector].

*Hyla regilla laticeps* Cope, 1889, p. 356 [syntypes, U.S.N.M. No. 5308 (7 specimens) from Cabo San Lucas, Baja California Sur, México; John Xanthus collector].

*Hyliola regilla* (part): Mocquard, 1889b, p. 339.

*Hyla regilla* (part): Smith and Taylor, 1948, p. 82.

*Hyla regilla curta*: Jameson, Mackey, and Richmond, 1966, p. 585.

**DIAGNOSIS:** This subspecies of *Hyla regilla* generally is more robust than *hypochondriaca* and has smooth skin on the dorsum, slightly more webbing on the feet, and slightly shorter hind limbs. Most specimens of *curta* tend to have more diffuse dorsal markings than do those of *hypochondriaca*.

**DESCRIPTION:** Males of this moderately small species attain a snout-vent length of 37.8 mm., and females reach 44.1 mm. Nine males from San Ignacio, Baja California Sur, México, have snout-vent lengths of 26.6 to 30.7 (mean, 28.2) mm.; the ratio of tibia length to snout-vent length is 0.460 to 0.500 (mean, 0.477); the ratio of foot length to snout-vent length is 0.442 to 0.489 (mean, 0.462); the ratio of head length to snout-vent length is 0.322 to 0.350 (mean, 0.334); the ratio of head width to snout-vent length is 0.326 to 0.361 (mean, 0.340), and the ratio of the diameter of the tympanum to that of the eye is 0.344 to 0.412 (mean, 0.386). Seven females from the same locality have snout-vent lengths of 26.8 to 38.0 (mean, 31.3) mm. and a proportionately larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.353 to 0.545 (mean, 0.440). Specimens from the southern part of the peninsula are somewhat larger and have a proportionately larger tympanum. Two males from Todos Santos, Baja California Sur, have snout-vent lengths of 35.8 and 37.8 mm.; in these specimens, the ratio of the diameter of the tympanum to that of the eye is 0.488 and 0.500. Two females from the same locality have snout-vent lengths of 41.6 and 44.6 mm.; in these specimens, the ratio of the diameter of the tympanum to that of the eye is 0.579 and 0.605.

The head is as wide as the body, and the top of the head is barely convex. In dorsal and lateral profiles, the snout is rounded. The snout is moderately long; the nostrils are noticeably protuberant at a point about two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is barely concave, and the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance less than the diameter of the tympanum.

The arms are moderately short and slender; an axillary membrane is absent. No distinct row of tubercles is present on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately short and bear rather small discs; the width of the disc on the third finger is somewhat less than the diameter of the eye. The subarticular tubercles are large and conical; none is bifid. The supernumerary tubercles are large, elevated, and conical. A distinct, bifid palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a small nuptial excrescence. Webbing on the hands is absent. The hind limbs are moderately short and robust. The heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A thin transverse dermal fold is present on the heel, and a distinct tarsal fold is present. The inner metatarsal tubercle is elevated, elliptical, and barely visible from above. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately large and conical, and the supernumerary tubercles are small, but distinct. The toes are about two-thirds webbed. The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the distal end of



the antepenultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs; a short, broad anal flap is present. The skin on the dorsum is smooth; that on the throat, belly, and proximal posteroventral surfaces of the thighs is granular. The tongue is broadly cordiform, shallowly notched posteriorly, and free behind for about one-third of its length. The denticulous processes of the prevomers are narrowly separated, transverse elevations between the posterior margins of the small, ovoid choanae. Males have four to six teeth on each process and a total of eight to eleven (mean, 9.8) prevomerine teeth. Females likewise have four to six teeth on each process and a total of eight to twelve (mean, 10.3) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

I have no knowledge of the coloration of *Hyla regilla curta* in life. In preservative the dorsum is dull grayish tan with darker grayish brown markings (pl. 1, fig. 3). All specimens have a distinct dark mark beginning on the snout and extending to the nostril and eye and posteriorly to the anterior part of the flank. In most individuals, this mark is bordered above by a narrow white line. The lips are pale grayish white. The markings consist of a pair of irregular dark dorsolateral marks, which are confluent anteriorly in some specimens. Most individuals possess a well-defined triangular mark on the top of the head. The dorsal surfaces of the limbs are faintly barred with dark brown, and the posterior surfaces of the thighs are dull tan. The flanks are pale gray with dark brown flecks or spots. A faint white anal stripe is present. The venter is creamy tan, and the vocal sac is heavily flecked with gray.

**TADPOLES:** The tadpoles of this subspecies are unknown; presumably they are like those of *Hyla regilla hypochondriaca*.

**MATING CALL:** The call of this subspecies consists of a series of short diphasic notes, "aah-aah, aah-aah, aah-aah." The analysis of the call of one individual from Todos Santos,

Baja California Sur, reveals that the note repetition rate is 30 notes per minute, and that the duration of the note is about 0.10 of a second; the fundamental frequency is at 121 cycles per second and the dominant frequency at 2420 cycles per second (pl. 12, fig. 1).

**NATURAL HISTORY:** I have had no first-hand field experience with this subspecies, nor has there been any published record concerning its ecology. The frogs apparently congregate around any depression containing moisture and breed there when sufficient water accumulates. Dr. Laurence M. Hardy obtained a calling male from a water-filled ditch at Todos Santos, on July 9, 1963, and he found several individuals in clumps of grass near an outlet from an artificial tank containing water.

**REMARKS:** Although the type specimens of *Hyla curta* and *Hyla regilla laticeps* are rather faded, there is no doubt but what they represent the same species of tree frogs. All workers in the present century have regarded *laticeps* and *curta* as synonyms of *Hyla regilla*. Jameson, Mackey, and Richmond (1966, p. 585) resurrected *Hyla curta* Cope, 1867, as a subspecies of *Hyla regilla*. On the basis of a sophisticated mathematical analysis of a variety of measurements of possible doubtful significance, those authors partitioned the widespread *Hyla regilla* into numerous subspecies. The populations of *regilla* in the southern part of Baja California seem to be moderately distinct from those populations to the north. Consequently, I am recognizing the southern population as *Hyla regilla curta*.

**ETYMOLOGY:** The subspecific name is derived from the Latin *curtus*, meaning short, and possibly refers to the length of the legs in this subspecies.

**DISTRIBUTION:** *Hyla regilla curta* occurs at elevations from sea level to approximately 1000 meters in the peninsula of Baja California south of the Desierto de Vizcaíno, México (fig. 247).

See Appendix 1 for the locality records of the 98 specimens examined.

#### *Hyla regilla hypochondriaca* Hallowell

*Hyla scapularis* var. *hypochondriaca* Hallowell, 1854, p. 97 [syntypes, U.S.N.M. 3235 (8 specimens) from Tejon Pass, Los Angeles County, California, U.S.A.; A. L. Heermann collector].

*Hyla regilla* (part): Smith and Taylor, 1948, p. 82.

*Hyla regilla deserticola* Jameson, Mackey, and Richmond, 1966, p. 582 [holotype, S.D.N.H.M. 54176 from San Borja, Baja California del Norte, México; David L. Jameson collector].

*Hyla regilla hypochondriaca*: Jameson, Mackey, and Richmond, 1966, p. 588.

**DIAGNOSIS:** This subspecies of *Hyla regilla* is more slender than *curta* and has slightly longer hind limbs and slightly less webbing. The skin on the dorsum is weakly pustulate in some specimens, whereas it is smooth in *curta*. The dorsal markings in *hypochondriaca* are more distinct than in *curta*.

**DESCRIPTION:** Males of this subspecies attain a snout-vent length of 37.1 mm., and females reach 38.2 mm. In a series of 25 males from Ramona, San Diego County, California, the snout-vent length is 27.8 to 36.9 (mean, 32.9) mm.; the ratio of tibia length to snout-vent length is 0.451 to 0.502 (mean, 0.477); the ratio of foot length to snout-vent length is 0.407 to 0.498 (mean, 0.452); the ratio of head length to snout-vent length is 0.312 to 0.346 (mean, 0.327); the ratio of head width to snout-vent length is 0.344 to 0.378 (mean, 0.359), and the ratio of the diameter of the tympanum to that of the eye is 0.424 to 0.624 (mean, 0.540).

Morphologically this subspecies is like *Hyla regilla curta*, except that the skin on the dorsum is weakly pustulate in some specimens. Most individuals possess a row of tubercles along the ventrolateral edge of the forearm. The webbing is vestigial or absent on the hands (fig. 243A), and the feet are somewhat more than one-half webbed (fig. 244A). Males have three to five teeth on each prevomerine process and a total of six to ten (mean, 7.2) prevomerine teeth.

Specimens from Ramona, San Diego County, California are highly variable in dorsal coloration (pl. 65, figs. 1-4). The dorsum is green with darker green markings, tan with brown markings, grayish tan with grayish brown markings, or reddish brown with dark brown markings. The flanks are creamy white, pale grayish tan with brown flecks. The groin, anterior and posterior surfaces of the thighs, the inner edges of the tarsi, the bases of the first and second toes, and the ventral surfaces of the hind limbs are dull yellow. There is a narrow white canthal and supratympanic white stripe and an indistinct white anal

stripe. A broad white labial stripe is present, a dark brown stripe extends from the tip of the snout, through the nostril and eye, and posteriorly to a point above the insertion of the arm; from that point it continues on to the flank as a series of brown spots in some specimens. The belly and ventral surfaces of the arms are creamy white. The vocal sac is dull yellow with greenish gray flecks. The iris is dull bronze with a median horizontal brown streak.

In preservative, the dorsum varies from pale bluish gray and yellowish tan to dull grayish brown. Most individuals have a pattern consisting of a pair of longitudinal dark brown stripes that are continuous or interrupted one or more times. All specimens have some form of a triangular dark mark between the eyes with the apex of the triangle directed posteriorly. The dorsal surfaces of the limbs are strongly banded with dark brown.

**TADPOLES:** A typical tadpole in developmental stage 35 has a body length of 12 mm. and a total length of 30 mm. The body is robust and as deep as wide. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is round. The eyes are widely separated and directed laterally. The nostrils are directed anterolaterally at a point somewhat closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point just below the midline about two-thirds of the distance from the tip of the snout to the posterior end of the body. The anal tube is dextral. The caudal musculature is slender and tapers gradually to the tip of the rounded tail. The fins are deep, at midlength of the tail, both the dorsal and ventral fins are about half again as deep as the caudal musculature. The dorsal fin extends onto the body (fig. 245A).

The coloration in life was described by Gaudin (1965, p. 122). He noted that in early developmental stages the body is rather evenly covered with melanophores and that golden chromatophores and a few guanophores are scattered over the dorsal and lateral parts of the body. He stated that the dorsal and lateral parts of the tail musculature have melanophores scattered throughout with a sprinkling of golden chromatophores and guanophores. Gaudin noted that in stage 30

the distribution of melanophores is relatively stable. He stated: "Anterior to the spiracle, melanophores occur in a rather heavy concentration dorsally and extend down to the ventral surface of the body, while posterior to the spiracle, melanophores extend only one-half to two-thirds of the distance down the sides of the body. The intestines are still completely obscured by an opaque layer of melanophores lining the coelom. Golden chromatophores and guanophores are scattered over the dorsal and lateral parts of the body and tail musculature and contribute varying amounts of sheen to the body, depending on the degree of contraction of the chromatophores."

In preservative, the tadpoles are dull brown above and transparent below. The caudal musculature is creamy tan with dense brown flecks, especially anteriorly. The fins are transparent and are flecked with brown above and distally on the ventral fin.

The mouth is moderately small and antero-ventral in position. The lips have a shallow lateral fold. The median half of the upper lip is bare; the lower lip is bordered by a single row of blunt papillae, but two rows of papillae are present laterally. The beaks are moderately robust and bear blunt serrations. The upper beak is in the form of a broad arch with robust, short lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length, and the second upper row is broadly interrupted medially. The first and second lower rows are nearly as long as the upper rows, whereas the third lower row is short (fig. 246A).

**MATING CALL:** The call of *Hyla regilla hypochondriaca* consists of a series of short, usually diaphasic notes (see Snyder and Jameson, 1965, p. 131) for a discussion of the variation in mating call in *Hyla regilla*).

**NATURAL HISTORY:** No observations on the natural history of this subspecies have been made in México; the reader is referred to a general account of the species by Stebbins (1951, 1: 322).

**REMARKS:** Although Jameson, Mackey, and Richmond (1966, p. 554) arrived at the conclusion that *hypochondriaca* was an available name for a population of *Hyla regilla* in southern California, they did so without the

benefit of examination of the type in question and miraculously were correct in their conclusions. Jameson, Mackey, and Richmond (1966) analyzed the variation in *Hyla regilla* and recognized ten computer-generated subspecies, some of which are distinguished on extremely superficial characters. I have been unable to justify the recognition of two subspecies of *Hyla regilla* in northern Baja California, México. Consequently, I conclude that *Hyla regilla deserticola* Jameson, Mackey, and Richmond, 1966, is a synonym of *Hyla regilla hypochondriaca* Hallowell, 1854.

**ETYMOLOGY:** The subspecific name is derived from the Greek, *hypochondriakos*, meaning literally of the abdomen. I am unsure of its reference to the frog concerned.

**DISTRIBUTION:** *Hyla regilla hypochondriaca* occurs at elevations from sea level to about 1400 meters from the northern end of the interior valley of California southward through southern California and extreme southern Nevada to the northern half of the peninsula of Baja California, México; the subspecies also occurs on the islands off the Pacific coast of California and Baja California (fig. 247).

See Appendix 1 for the locality records of the 109 specimens examined.

### *Hyla cadaverina* Cope

*Hyla arenicolor* (part): Kellogg, 1932, p. 156. Smith and Taylor, 1948, p. 89.

*Hyla nebulosa* Hallowell, 1854, p. 96 [syntypes, A.N.S.P. Nos. 1987 and 1988 from Tejon Pass, Los Angeles County, California, U.S.A.; A. L. Heermann collector (not *Hyla nebulosa* Spix, 1824, from Brazil)].

*Hyla cadaverina* Cope, 1866a, p. 84 [replacement name for *Hyla nebulosa* Hallowell, 1854, preoccupied by *Hyla nebulosa* Spix, 1824]. Duellman, 1968c, p. 200.

*Hyla californiae* Bogert, 1958, p. 11 [nomen nudum].

*Hyla californiae* Gorman, 1960, p. 214 [holotype, M.V.Z. No. 31773 from Cañon de Llanos, 9 miles south-southwest of "Alaska" (La Rumorosa), Baja California del Norte, México; Robert R. Miller and J. Davis collectors].

**DIAGNOSIS:** This moderately small species has tubercular skin on the dorsum and lacks webbing on the hand; the feet are about three-fourths webbed. The dorsum is gray or brown with numerous small, irregular spots. This species differs from all other members of the



*eximia* group by having a distinctly tuberculate dorsum, small dorsal spots, and no dark brown band on the side of the head posteriorly onto the body. *Hyla cadaverina* differs from *regilla* by being more pustulate and by having more webbing on the feet (web to base of penultimate phalanx of the fourth toe in *cadaverina* and only to base of antepenultimate phalanx in *regilla*). *Hyla cadaverina* resembles *arenicolor*, which is somewhat larger and differs by having less webbing on the feet (about one-half webbed), larger discs, more numerous and distinct supernumerary tubercles, and a larger tympanum; the diameter of the tympanum in *cadaverina* is about half of the diameter of the eye, whereas in *arenicolor* it is about two-third of the diameter of the eye. Other Middle American hylids that might be confused with *cadaverina* all have webbing between the fingers.

**DESCRIPTION:** Males of this moderately small species attain a snout-vent length of 36.0 mm., and females reach 45.0 mm. In a series of 16 males from Boulder Park, San Diego County, California, the snout-vent length is 29.0 to 35.9 (mean, 33.0) mm.; the ratio of tibia length to snout-vent length is 0.474 to 0.523 (mean, 0.503); the ratio of foot length to snout-vent length is 0.432 to 0.477 (mean, 0.447); the ratio of head length to snout-vent length is 0.334 to 0.368 (mean, 0.354); the ratio of head width to snout-vent length is 0.383 to 0.417 (mean, 0.397), and the ratio of the diameter of the tympanum to that of the eye is 0.432 to 0.529 (mean, 0.478). Nine females from the same locality have snout-vent lengths of 39.4 to 43.9 (mean, 40.9) mm. and do not differ significantly in proportions.

The head is slightly broader than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded; in lateral profile it is round. The canthus is round and barely evident; the loreal region is slightly concave and the lips are moderately thick and not flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point just posterior to the angle of the jaw. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from

the eye by a distance equal to about one-half of the diameter of the tympanum.

The arms are moderately short and slender; no axillary membrane is present. A row of low tubercles is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear relatively small discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The discs are truncate. The subarticular tubercles are moderately large and conical; in some individuals one or more tubercles are bifid. The supernumerary tubercles are small and conical. A large, flat palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a weak nuptial excrescence. Webbing is absent between the fingers (fig. 243B). The hind limbs are moderately short and slender; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the eye. A weak tarsal fold is evident distally on the tarsus; a few small tubercles are present on the outer edge of the tarsus. The inner metatarsal tubercle is moderately small, ovoid and flat. No outer metatarsal tubercle is evident. The toes are moderately long and slender and bear small discs. The subarticular tubercles are small and conical, and the supernumerary tubercles are minute. The toes are about three-fourths webbed (fig. 244B). The webbing extends from the base of the penultimate phalanx of the first toe to the middle of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs; a short anal sheath is present. The skin on the dorsum has numerous scattered tubercles; that on the throat, chest, and proximal posteroventral surfaces of the thighs is granular. Elsewhere, the skin is smooth. The tongue is narrowly cordiform, shallowly notched posteriorly, and barely free behind. The denticulous processes of

the prevomers are small ovoid elevations between the round choanae. Males have two to four teeth on each process and a total of four to seven (mean, 6.1) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue towards the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla cadaverina* is dull grayish brown or olive-brown with darker spots dorsally (pl. 64, fig. 1). In living individuals from San Diego County, California, the dorsum is dull olive-brown with dull olive-green spots on the back and bars on the limbs. The flanks are pale olive-tan with dull olive-green flecks. The groin, anterior surfaces of the thighs, ventral surfaces of the shanks, and the inner surfaces of the tarsi are pale dull yellow. The posterior surfaces of the thighs are a darker dull yellow. The anterior part of the throat is dark gray with white flecks; the posterior part of the throat and the belly are pale white. A narrow silvery cream labial stripe is present. The iris is pale bronze with black reticulations and a median horizontal brown streak.

In preservative the dorsum varies from dull gray to dull brown with darker markings, which consist of small irregular spots scattered over the dorsum and transverse bars on the dorsal surfaces of the limbs. The flanks are pale tan or pale gray with small dark flecks. The venter is dull white, and the posterior surfaces of the thighs are creamy tan. A faint white anal stripe is present and numerous white tipped tubercles are evident in the anal region.

**TADPOLES:** A typical tadpole in developmental stage 25 has a body length of 8.2 mm. and a total length of 18.2 mm. The body is as wide as deep; the snout in dorsal profile is bluntly rounded and in lateral profile, it is round. The eyes are moderately small, broadly separated, and directed laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point slightly below the midline at about two-thirds of the distance from the tip of the snout to the posterior end of the body. The anal tube is short and dextral. The caudal musculature is slender and does not extend to the tip of

the bluntly rounded tail. The caudal fins are deep; at midlength of the tail, the depth of the dorsal fin is half again the depth of the caudal musculature. The dorsal fin does not extend on to the body (fig. 245B).

In life the dorsal and lateral surfaces of the body are dark brown, whereas the venter has a yellowish or cream tinge. Dark irregular blotches are present on the caudal musculature. A few brown flecks are present on the dorsal fin. In preservative, the tadpoles are pale brown; the caudal musculature is creamy tan with dark brown blotches tending to form transverse bands on the dorsal surface of the musculature.

The mouth is moderately small and directed anteroventrally. Weak lateral folds are present in the lips. The median two-thirds of the upper lip is bare; elsewhere, the lips are bordered by a single row of large, elongate papillae. The beaks are moderately slender and bear long, blunt serrations. The upper beak is in the form of a high, acutely rounded arch with long, slender lateral processes; the lower beak is broadly U-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length, and the second upper row is broadly interrupted medially. The first and second lower rows are equal in length and somewhat shorter than the upper rows, whereas the third lower row is much shorter than the others (fig. 246B).

Gaudin (1964) described the tadpole of this species under the name of *Hyla californiae*. In 1965, he compared the larval development of this species with that in *Hyla regilla*.

**MATING CALL:** The call of *Hyla cadaverina* consists of a long series of short notes: "aah-aah-aah." The analysis of recordings of four individuals from Sentenae Cañon, San Diego County, California, reveals that the note repetition rate is 44 to 50 (mean, 46.7) notes per minute and that the notes have a duration of 0.12 to 0.15 (mean, 0.135) of a second. The pulse rate is 125 to 135 (mean, 131.2) pulses per second. The fundamental frequency varies from 130 to 137 (mean, 131.7) cycles per second and the dominant frequency varies from 2055 to 2080 (mean, 2073) cycles per second (pl. 12, fig. 2).

**NATURAL HISTORY:** According to Gorman

(1960, p. 220) *Hyla cadaverina* occurs in canyons where they are rarely found in trees, but usually are found on rocks adjacent to pools of water in the bottom of the canyon. The frogs breed following rain storms from Mid-March to mid-June.

REMARKS: Duellman (1968c, p. 200) discussed the allocation of the specific name *cadaverina*, which is a replacement name for *Hyla nebulosa* Hallowell, 1854, preoccupied by *Hyla nebulosa* Spix, 1824. For many years *Hyla cadaverina* masqueraded as a western population of *Hyla arenicolor*. Bogert (1950, p. 11) showed that the California populations of "*Hyla arenicolor*" had a distinctively different call from that of *Hyla arenicolor* east of the Mojave and Colorado deserts. Gorman (1960, p. 214) named the western population *Hyla californiae*, a name that has been used subsequent to 1960, until Duellman (1968c, p. 200) showed that *cadaverina* was an earlier name for the western population of tree frogs that characteristically inhabits canyons.

ETYMOLOGY: The specific name is derived from the Latin *cadaver*, meaning corpse, and the diminutive suffix *-ina* and means literally, little corpse, possibly in allusion to the pallid appearance of the species.

DISTRIBUTION: *Hyla cadaverina* occurs at elevations usually less than 500 meters in the mountains of the southern part of California in the United States and in the northern part of the peninsula of Baja California, México (fig. 248).

See Appendix 1 for the locality records of the 44 specimens examined.

### *Hyla plicata* Brocchi

*Hyla plicata* Brocchi, 1877b, p. 126 [holotype, M.N.H.N. No. 6317 from "México"; Marie-Firmin Bocourt collector]; 1882, p. 35. Boulenger, 1882a, p. 396. Günther, 1901 (1885-1902), p. 261. Kellogg, 1932, p. 173. Smith and Taylor, 1948, p. 88. Duellman, 1968c, p. 201.

*Hyla lafrentzi* Mertens and Wolterstorff, 1929, p. 235 [holotype, M.M. No. 49/27 from Desierto de los Leones, Distrito Federal, México; K. Lafrentz collector (holotype destroyed; S.N.M. No. 30997 from the same locality designated as neotype by Jameson, Mackey, and Richmond, 1966, p. 596)]. Smith and Taylor, 1948, p. 84.

*Hyla gracilipes*: Kellogg, 1932, p. 168.

*Hyla regilla lafrentzi*: Jameson, Mackey, and Richmond, 1966, p. 596.

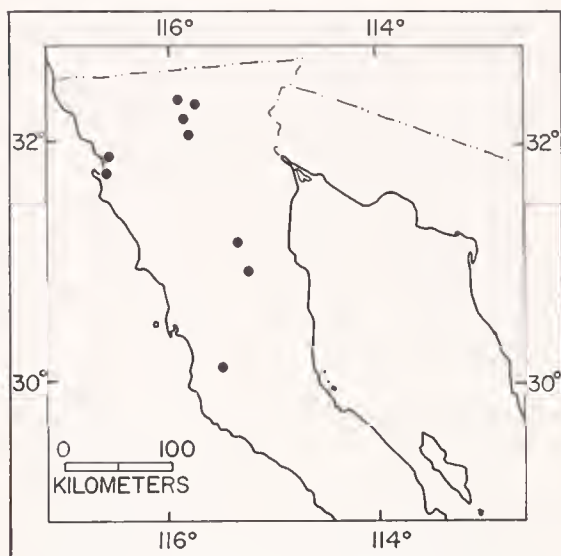


FIG. 248. Distribution of *Hyla cadaverina* in México.

DIAGNOSIS: This medium-sized green frog has a brown face and brown postorbital band extending to midflank, bordered above by a narrow white line; the fingers lack webbing; and the toes are about two-thirds webbed, and the discs are small. The posterior surfaces of the thighs are uniform brown, and the dorsal surfaces usually are uniform green. The smooth skin on the dorsum and absence of many small irregular spots or a large interorbital triangular mark distinguish *plicata* from *cadaverina* and *regilla*. *Hyla euphorbiacea* differs by having many yellow spots on the posterior surfaces of the thighs. *Hyla eximia* and *walkeri* are slightly smaller (males to 36 mm. as compared with 44 mm. in *plicata*) and have slightly less webbing on the feet; the web usually extends only to the distal end of the antepenultimate phalanx of the fifth toe in *eximia* and *walkeri*, whereas it extends to the base of the penultimate phalanx in *plicata*. The dorsum in *plicata* is green with or without a pair of dorsolateral brown longitudinal marks posteriorly; the dorsum in *walkeri* is similarly marked in most specimens, whereas the dorsal pattern in *eximia* usually consists of dark stripes and/or spots.

DESCRIPTION: Males of this medium-sized species attain a snout-vent length of 44.0 mm., and females reach 47.4 mm. In a series of 15 males from El Chico Parque Nacional, Hi-



dalgo, México, the snout-vent length is 36.7 to 41.6 (mean, 39.7) mm.; the ratio of tibia length to snout-vent length is 0.482 to 0.570 (mean, 0.501); the ratio of foot length to snout-vent length is 0.449 to 0.525 (mean, 0.479); the ratio of head length to snout-vent length is 0.291 to 0.316 (mean, 0.306); the ratio of head width to snout-vent length is 0.337 to 0.379 (mean, 0.360), and the ratio of the diameter of the tympanum to that of the eye is 0.500 to 0.650 (mean, 0.570). Five females from the same locality have snout-vent lengths of 37.9 to 47.4 (mean, 43.8) mm. and a proportionately larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.590 to 0.684 (mean, 0.613). In a series of 25 males from San Gregorio, Michoacán, México, the snout-vent length is 32.7 to 39.0 (mean, 36.7) mm., and the ratio of the diameter of the tympanum to that of the eye is 0.444 to 0.583 (mean, 0.504). Although the frogs from San Gregorio are smaller and have a proportionately smaller tympanum than those from El Chico, the other proportions are nearly the same.

The head is slightly narrower than the body, and the top of the head is barely convex. The eyes are large and prominent. The snout in dorsal profile is rounded; and in lateral profile it is bluntly rounded. The snout is short; the nostrils are protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded but evident, and the loreal region is noticeably concave; the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point behind the angles of the jaws. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum. The arms are moderately short and somewhat robust; an axillary membrane is absent. A row of low tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about three-fifths of the diameter of the eye. The subarticular tuber-

cles are large and round; none is bifid. The supernumerary tubercles are large and conical. A large, elevated partially bifid palmar tubercle is present. The prepollex is moderately enlarged and bears a horny nuptial excrecence in breeding males. Webbing is absent between the fingers (fig. 243F). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin transverse dermal fold is present on the heel, and a strong flap-like tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately large, flattened, and elliptical. A conical outer metatarsal tubercle is present. The toes are long and slender and bear small discs. The subarticular tubercles are moderately large and round, and the supernumerary tubercles are large, subconical, and numerous on the proximal segments of each digit. The toes are about two-thirds webbed (fig. 244F). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs; it is covered by a short, broad anal sheath. The skin on the dorsum is smooth; that on the throat, belly, and posteroventral surfaces of the thighs is heavily granular. The tongue is eordiform, shallowly notched behind, and barely free posteriorly. The denticulous processes of the prevomers are small, transverse or slightly posteromedially inclined, narrowly separated elevations between the anterior margins of the small, ovoid choanae. Males have four to six teeth on each process and a total of 8 to 12 (mean, 10.3) prevomerine teeth. Females have five to seven teeth on each process and a total of 10 to 14 (mean, 11.8) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the

mouth. The vocal sac is single, median, and subgular.

The general coloration of *Hyla plicata* is dark green with a brown lateral stripe (pl. 66, fig. 2). In most individuals the dorsum is dark green and is marked only by a dorso-lateral brown stripe or series of dashes connecting in the sacral region and extending to, or nearly to, the vent. A dark brown stripe extends from the tip of the snout, through the nostril, eye, and tympanum, and thence onto the flank; in most individuals, the brown stripe is continuous to the groin. The brown stripe is bordered above by a narrow white line. The outer edges of the feet, shanks, and forearms are dark brown, bordered above by narrow white lines. A faint white anal stripe and a narrow white labial stripe are present. The posterior surfaces of the thighs are uniform dull tan, and the venter is creamy white. The vocal sac in breeding males is gray with white flecks. The iris is dull bronze.

In preservative the dorsum is dark bluish gray, and the venter is creamy tan. The posterior surfaces of the thighs are dull tan to dark brown. The dark markings on the side of the head and body are present in all specimens. The only noticeable variation in color pattern is in the dorsal markings, which are absent in some specimens. A few individuals have a dark brown stripe extending anteriorly to the scapular region, and in some specimens small round, brown spots are present posteriorly on the dorsum in addition to the longitudinal brown markings.

**TADPOLES:** The only tadpoles available for this species are recently hatched ones that are unusable for description of the larval characteristics.

**MATING CALL:** The call of *Hyla plicata* consists of a long, low note, "waah." The analysis of calls of three individuals revealed the presence of four to 16 notes in a call-group and a note repetition rate of 24 to 60 (mean, 40) notes per minute. The duration of the notes varies from 0.52 to 0.72 (mean, 0.63) of a second, and the pulse rate varies from 78 to 98 (mean, 90) pulses per second. The fundamental frequency varies from 83 to 109 (mean, 96) cycles per second, and the dominant frequency varies from 1328 to 1632 (mean, 1495) cycles per second (pl. 14, fig. 3).

**NATURAL HISTORY:** *Hyla plicata* inhabits humid pine and fir forests. At El Chico Parque Nacional, Hidalgo, México, in the month of June in 1960, 1962, and 1966, calling males were found on rocks in the surface of the water in a quiet pool in a stream in a meadow, on junipers and bunch grass at the edge of a meandering stream in a meadow and from the ground at the edge of a shallow pond. A clasping pair was observed in the water of a shallow pond in the meadow on June 16, 1966; the following morning a clutch of eggs was found attached to sticks in the water. Taylor (1939b, p. 436) stated: "The specimens collected near Vigas, Veraacruz, were found about a small rainpool beside the highway during the morning. The males were calling. Those taken at Zempoala were calling most of the day. A single pair was found clasping. A few immature tadpoles, presumably of this species were found in small pools in the bog near the lake edge."

Duellman (1961e, p. 50) reported adults and recently metamorphosed young from beneath logs and rocks in a damp canyon on the west slope of Cerro San Andrés, Michoacán, México, in March. The limited observations on breeding sites suggest that this species probably utilizes small temporary pools in montane meadows as well as quiet pools in the streams. It is highly unlikely that the tadpoles are adapted for life in torrential streams.

**REMARKS:** Duellman (1968e, p. 201) resurrected Brocchi's name *Hyla plicata* for those frogs that had been known as *Hyla lafrentzi* Mertens and Wolterstorff. Jameson, Mackey, and Richmond (1966, p. 596) placed *lafrentzi* (= *plicata*) as a subspecies of *Hyla regilla*. Duellman (1968e, p. 203) noted the extreme differences in mating calls, as well as different morphological characters between *regilla* and *plicata* and concluded that *plicata* was a species distinct from *regilla* and from *eximia*, which occurs sympatrically with *lafrentzi* in the lower part of the range of the latter.

Jameson, Mackey, and Richmond (1966, p. 555) suggested that *Hyla cardenasi* was a synonym of *Hyla lafrentzi* (= *plicata*). Examination of the type specimen of *cardenasi* reveals that it is identical with *eximia*; therefore, the suggestion of these authors should be disregarded.

**ETYMOLOGY:** The specific name is Latin, meaning folded; I am uncertain as to the significance of the name with reference to this species of frog.

**DISTRIBUTION:** *Hyla plicata* occurs principally at high elevations (2400 and 3600 meters) in pine and fir forest in the mountains of the Sierra Madre Oriental and the Cordillera Volcánica along the southern edge of the Mexican Plateau (fig. 249). The species occurs at somewhat lower elevations on eastern slopes of the Sierra Madre Oriental in central Veracruz, where specimens have been obtained between 1400 and 1500 meters in the vicinity of Vigas.

See Appendix 1 for the locality records of the 403 specimens examined.

### *Hyla eximia* Baird

*Hyla eximia* Baird, 1854, p. 61 [syntypes, U.S.N.M. No. 3248 (2 specimens) from "Valley of México," (Distrito Federal), México; William Rich collector]. Brocchi, 1882, p. 32. Boulenger, 1882a, p. 378. Günther, 1901 (1885-1902), p. 261. Kellogg, 1932, p. 164. Smith and Taylor, 1948, p. 83.

*Hyla gracilipes* Cope, 1865b, p. 194 [syntypes, U.S.N.M. No. 15318-15321 from Mirador, Veracruz, México; Charles Sartorius collector]. Brocchi, 1882, p. 36. Boulenger, 1882a, p. 378. Günther, 1901 (1885-1902), p. 262. Kellogg, 1932, p. 168.

*Hyla eximia eximia*: Cope, 1887, p. 14.

*Hyla cardenasi* Taylor, 1939b, p. 430 [holotype, U.S.N.M. No. 84403 from Puebla, Puebla, México; H. Ruano collector]. Smith and Taylor, 1948, p. 83.

*Hyla wrightorum* Taylor, 1939b, p. 436 [holotype,

U.M.M.Z. 79141 from 11 miles south of Springerville, Apache County, Arizona, U.S.A.; Irving J. Cantrall collector]. Smith and Taylor, 1948, p. 84.

*Hyla arboreola* Taylor, 1941, p. 118 [holotype, F.M.N.H. No. 100131 (formerly E.H.T.-H.M.S. No. 24556) from 6 miles east of Omilteme, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 83.

*Hyla eximia wrightorum*: Schmidt, 1953, p. 71.

*Hyla microeximia* Maslin, 1957, p. 81 [holotype, U.S.N.M. No. 139246 from 3 miles northwest of Joco-tepec, Jalisco, México; T. Paul Maslin collector].

*Hyla regilla wrightorum*: Jameson, Mackey, and Richmond, 1966, p. 594.

**DIAGNOSIS:** This moderately small species with smooth dorsal skin, small discs, no webbing between the fingers, and the toes about two-thirds webbed has a brown face mask, uniformly tan posterior surfaces of the thighs, and a green dorsum that is variously marked with a linear arrangement of brown spots or stripes in most specimens. *Hyla eximia* differs from *cadaverina* in color (green instead of brown or gray) and in lacking the tubercular skin of *cadaverina*. *Hyla regilla* can be distinguished from *eximia* by the presence in the former of a dark interorbital triangular-mark and dark spots or flecks on the flanks; in *eximia* the dorsal and lateral color is separated by a narrow white line, below which the flanks are uniform creamy tan. *Hyla euphorbiacea* differs from *eximia* by having yellow spots on the posterior surfaces of the thighs. *Hyla plicata* and *walkeri* are extreme-

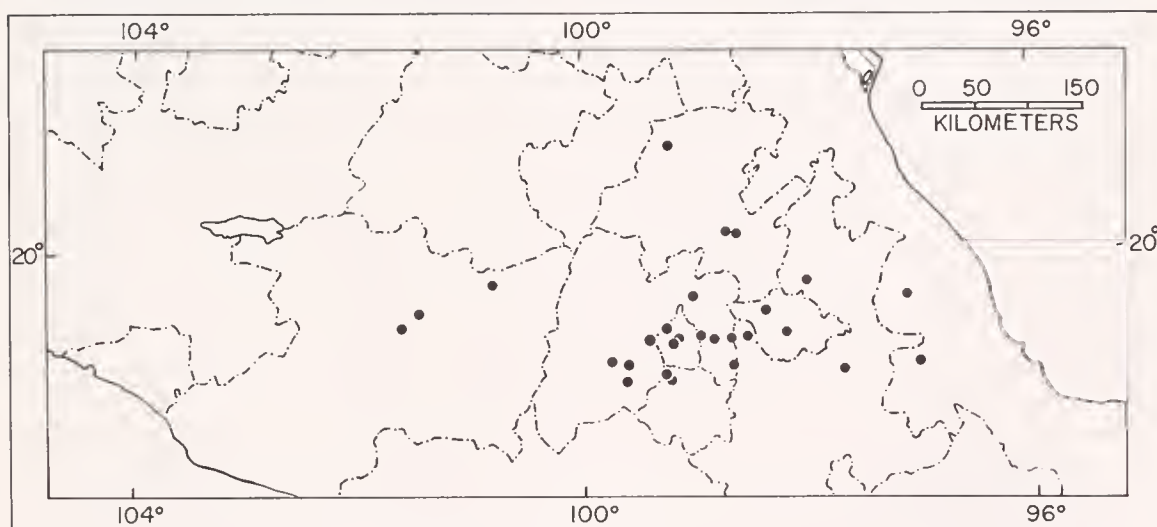


FIG. 249. Distribution of *Hyla plicata*.



ly difficult to distinguish from *eximia*; both usually lack transverse bars on the dorsal surfaces of the thighs and either lack dorsal markings or have only a pair of short brown lines posteriorly. In most specimens of *eximia* transverse bars are present on the thighs and the dorsum is marked by spots and/or dark lines. *Hyla plicata* is larger (males to 44 mm.) than *eximia* (35 mm.).

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 35.0 mm., and females reach 36.2 mm. In a series of 25 males from 3.2 kilometers west of Arandes, Jalisco, México, the snout-vent length is 24.6 to 30.9 (mean, 27.8) mm.; the ratio of tibia length to snout-vent length is 0.432 to 0.495 (mean, 0.457); the ratio of foot length to snout-vent length is 0.427 to 0.478 (mean, 0.446); the ratio of head length to snout-vent length is 0.278 to 0.326 (mean, 0.307); the ratio of head width to snout-vent length is 0.304 to 0.371 (mean, 0.337), and the ratio of the diameter of the tympanum to that of the eye is 0.500 to 0.680 (mean, 0.572). Three females from the same locality have snout-vent lengths of 27.2 to 29.4 (mean, 28.5) mm. They exhibit no significant differences in proportions from the males. A mosaic of minor variation in sizes and proportions exist throughout the range of this species; this variation is illustrated in part by five samples (table 47).

The head is narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded; in lateral profile it is round. The snout is moderately long; the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is barely concave; the lips are moderately thin and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point posterodorsal to the angles of the jaws. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about one-half of the diameter of the tympanum.

The arms are moderately short and slender; an axillary membrane is absent. A row of low, inconspicuous tubercles is present on

the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about three-fifths of the diameter of the tympanum. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are conical, conspicuous, and numerous on the proximal segments of each digit. An elevated palmar tubercle is present. The prepollex is moderately large and in breeding males lacks a horny nuptial excrescence. Webbing is absent on the hands (fig. 243C). The hind limbs are short and moderately robust; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the tympanum or to the posterior corner of the eye. A thin transverse dermal fold is present on the heel, and a strong tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is elevated and ovoid. A small conical outer metatarsal tubercle usually is evident. The toes are long and slender and bear discs that are about the same size as those on the fingers. The subarticular tubercles are moderately large and conical, and the supernumerary tubercles are small and usually evident only on the proximal segments of each digit. The toes are a little more than one-half webbed (fig. 244C). The webbing extends from the base of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the distal end of the antepenultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the distal end of the antepenultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper edge of the thighs; a short anal sheath is present. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is cordiform, shallowly notched posteriorly and free behind for about one-fourth of its length. The denticerous processes of the prevomers are small, widely separated medially, posteromedially inclined processes between the small ovoid choanae.

TABLE 47  
Variation in Size and Proportions, with Means in Parentheses, of Males of *Hyla eximia*.

Locality	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
El Salto, Durango	19	26.8-32.3 (29.4)	0.462-0.511 (0.481)	0.444-0.496 (0.471)	0.294-0.346 (0.313)	0.326-0.367 (0.345)	0.500-0.667 (0.560)
La Joya de Salas, Tamaulipas	25	29.2-34.9 (30.6)	0.467-0.524 (0.489)	0.456-0.504 (0.479)	0.277-0.317 (0.301)	0.312-0.348 (0.330)	0.474-0.581 (0.529)
Arandes, Jalisco	25	24.6-30.9 (27.8)	0.432-0.495 (0.457)	0.427-0.478 (0.446)	0.278-0.326 (0.307)	0.304-0.471 (0.337)	0.500-0.680 (0.572)
Ciudad Hidalgo, Michoacán	25	25.6-31.4 (28.0)	0.438-0.495 (0.465)	0.436-0.492 (0.457)	0.277-0.313 (0.301)	0.312-0.361 (0.339)	0.518-0.667 (0.566)
Puebla, Puebla	25	28.4-33.0 (30.4)	0.430-0.498 (0.463)	0.415-0.496 (0.456)	0.274-0.322 (0.294)	0.296-0.352 (0.326)	0.481-0.692 (0.592)

TABLE 48  
Variation in Dorsal Color Pattern in *Hyla eximia*.  
(Figures are proportions of sample.)

Sample	N	Lateral Light Stripe			Dorsal Dark Stripes		Dorsal Spots				
		Axilla	Flank	Groin	Absent	Posterior	Fragmented	Solid	Absent	Posterior	All Over
Chihuahua	42	0.40	0.38	0.22	0.64	0.33	0.03	0.00	0.48	0.52	0.00
Durango	70	0.07	0.46	0.47	0.60	0.14	0.26	0.00	0.16	0.10	0.74
Tamaulipas	43	0.00	0.14	0.86	0.63	0.07	0.30	0.00	0.05	0.07	0.88
Jalisco	87	0.00	0.37	0.63	0.28	0.16	0.40	0.16	0.18	0.53	0.29
Michoacán	72	0.00	0.25	0.75	0.02	0.17	0.39	0.42	0.56	0.39	0.05
Puebla	43	0.00	0.51	0.49	0.28	0.26	0.39	0.07	0.66	0.18	0.16

Males have three to five teeth on each process and a total of six to ten (mean, 8.1) prevomerine teeth; females have three to six teeth on each process and a total of 6 to 11 (mean, 8.5) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla eximia* is bright green above, usually with dark brown spots or dashes, and a dark brown lateral stripe (pl. 65, fig. 5; pl. 66, figs. 1 and 3). All individuals have a green dorsal ground color. This varies from a bright pale green to dark green or green with a tint of tan. A dark brown stripe begins on the snout and passes through the nostril, eye, and tympanum to extend onto the flank, as far as the groin in some specimens. This brown stripe is bordered above by a narrow white line. The posterior surfaces of the thighs are dull brown. The dorsal surfaces of the upper arms, thighs, shanks, and feet are marked by transverse dark brown bands or spots. The dorsal markings are highly variable. Some individuals lack dark markings on the dorsum, but in most there is some form of a dorsolateral series of dashes or a dorsolateral stripe. In addition to these marks, or in place of them, the dorsum in some individuals is marked by numerous small brown spots. The venter is creamy white, and the vocal sac in breeding males is dusty yellow with white flecks. The iris is dull bronze.

Three aspects of the color pattern were analyzed in six samples from throughout the range of the species (table 48). The lateral light stripe usually extends to the middle of the flanks or to the groin, but in specimens from the northern part of the range (Chihuahua) the stripe extends only to the axilla in 40 per cent in a sample of 42 specimens. On the other hand, in a series from Tamaulipas the lateral light stripe extends to the groin in 86 per cent of a sample of 43 specimens. In samples from the northern part of the range (Chihuahua, Durango, and Tamaulipas) the dorsal dark stripes are absent in more than 60 per cent of the specimens, whereas the stripes are solid in 42 per cent or fragmented in 39 per cent of the frogs in a sample of 72 specimens from Michoacán. Small spots are

present on the dorsum in some specimens. Most individuals from the southern part of the range (Michoacán and Puebla) lack dorsal spots, and few individuals from there have spots all over the dorsum. However, in samples from Durango, and Tamaulipas, small spots are present over most of the dorsum in more than three-fourths of the frogs examined. Uniformly green frogs are present throughout the range; Holman (1965, p. 34) noted the uniformly green frogs in a sample from Durango and postulated a polymorphic gene in this species.

In preservative, the dorsum is bluish gray. The anterior and posterior surfaces of the thighs, the groin, and the ventral surfaces of the limbs are creamy tan. The belly is creamy white, and the vocal sac in most breeding males is dark gray. The dorsal markings and the lateral stripe are dark brown. A distinct white anal stripe and labial stripe usually are evident.

**TADPOLES:** Series of tadpoles are available from various parts of the range of the species. Although some variation in pigmentation, particularly on the tail, is evident, the tadpoles in the various samples are very nearly alike. Series of tadpoles have been examined from Arizona, Durango, Nayarit, and Jalisco.

A typical tadpole in developmental stage 37 from Buenos Aires, Durango, México has a body length of 14.4 mm. and a total length of 32.1 mm. The body is deep; in dorsal profile the snout is bluntly rounded, and in lateral profile it is inclined anteroventrally from a point above the nostrils. The eyes are relatively small, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point somewhat closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point on the midline about three-fifths of the distance from the tip of the snout to the posterior end of the body. The anal tube is long and dextral. The caudal musculature is slender and tapers gradually to the tip of the acutely rounded tail. The fins are deep; at midlength of the tail the depth of the dorsal fin is slightly greater than that of the ventral fin and is equal to about twice the depth of the caudal musculature. The dorsal fin extends onto the body (fig. 245C).



The dorsal and lateral surfaces of the body are brown with minute silvery gold flecks. The venter is dark with an overlying tinge of pale gold. The caudal musculature is pale tan with dark brown flecks, especially concentrated on the dorsal aspect of the posterior two-thirds of the caudal musculature. The fins are transparent with dark flecks and reticulations on all of the dorsal fin and on the posterior two-thirds of the ventral fin. In preservative, the gold tinge on the venter and the silvery gold flecks on the dorsum are lost.

The mouth is small and directed antero-ventrally. Lateral folds in the lip are absent, and the median half of the upper lip is bare. The lips are bordered by two rows of small papillae; the beaks are rather massive and bear short serrations. The upper beak forms a broad arch with long, slender lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The two upper rows are equal in length, and the second upper row is narrowly interrupted medially. The first and second lower rows are slightly shorter than the upper rows, and the first lower row is narrowly in-

terrupted medially in some specimens. The third lower row is extremely short (fig. 246C).

Tadpoles from 40 kilometers northeast of Lagos de Moreno, Jalisco, México, were colored like those from Buenos Aires, Durango, but were more pallid in appearance; they lack dark pigmentation on the caudal musculature and fins. Zweifel (1961) presented a detailed description of the development of the tadpoles from the northern part of the range; he discussed these under the name of *Hyla wrightorum*.

**MATING CALL:** The mating call of *Hyla eximia* consists of a series of short, relatively low-pitched notes; in the calls of some individuals these notes are distinct and separated, whereas in others they are so closely spaced that the call resembles a trill. No typical call can be described, because the variation in each of the parameters of the call seems to vary independently from the others (table 49). Some individuals emit a slow call, and others have a fast call, whereas specimens from some areas emit an intermediate type of call (pl. 13).

Blair (1960) first pointed out the variation in the call of *Hyla eximia*; he noted the exis-

TABLE 49  
Geographic Variation in the Mating Calls of *Hyla eximia*.  
(Means are given in Parentheses.)

Locality	N	Repetition Rate (min.)	Duration Notes (sec.)	Pulse Rate (per sec.)	Frequencies (cps)	
					Fundamental	Dominant
Apache County Arizona	3	42-84 (68)	0.16-0.18 (0.167)	110-120 (115)	109-122 (118)	1635-2078 (1889)
Buenos Aires, Durango	3	42-60 (51)	0.39-0.42 (0.400)	80-85 (82)	74-87 (82)	1740-1826 (1781)
Tepic, Nayarit	1	58	0.20	60	87	1560
Lagos de Moreno, Jalisco	7	90-137 (119)	0.15-0.19 (0.170)	110-130 (120)	90-131 (123)	2034-2498 (2271)
Queretaro, Querctaro	1	156	0.15	100	83	2158
Huachinango, Puebla	3	88-96 (92)	0.24-0.25 (0.247)	70-80 (75)	89-111 (98)	2112-2221 (2184)
Pátzcuaro, Michoacán	1	92	0.23	95	100	2300
Toluca, México	2	90	0.21-0.24 (0.225)	78-80 (79)	77-91 (84)	2233-2462 (2297)
Sanctorium, Tlaxcala	3	45-60 (54)	0.28-0.30 (0.290)	48-52 (50)	87-91 (89)	2349-2457 (2297)
Ixtapán de la Sal, México	10	40-57 (47)	0.15-0.24 (0.200)	48-70 (55)	81-113 (103)	2300-2704 (2501)

tence of slow-calling populations and of other fast-calling populations. He suggested that possibly two or more species were involved. Bogert (1960, l. 296) stated: "Even with the limited information thus far obtained for a few representative populations of *Hyla eximia* . . . it is possible to show that intermediate stages ranging from an un-trilled to trilled calls may occur within populations currently assigned, and correctly so in all probability, to a single species. The variation within these populations . . . do not appear to be clinal in nature. On the contrary, the variations more closely resemble a mosaic pattern of distribution, insofar as can be judged by representative calls from seven populations." The recordings that I have analyzed provide data in support of Bogert's suggestion. However, I have been able to obtain data from only 34 recordings from 10 different samples. Much more work needs to be done on this aspect of the biology of *Hyla eximia*.

**NATURAL HISTORY:** *Hyla eximia* inhabits subhumid highlands, where it occurs in mesquite-grassland, scrub forests, and pine-oak forest. The species is an opportunistic breeder and utilizes shallow rainpools in undisturbed as well as artificial situations. Calling males have been found as early as June 11 and as late as August 21 on the Mexican Plateau. Breeding usually takes place in the shallow grassy ponds. The males call from shallow water or while floating on the surface of the water usually grasping a blade of grass or a stick with the hands. The eggs are laid in loose clumps attached to grasses in shallow water.

In December, 1959, adults were found secreted in bromeliads growing on pine trees near Tianguistengo, Hidalgo, México. Holman (1965, p. 34) reported finding adults and many juveniles beneath rocks in pine forests at La Ciudad, Durango, México, in March.

The tadpoles develop in shallow grassy ponds, where they seek refuge amidst the aquatic vegetation. Tadpoles have been found as early as June 27 near Ixtapán de la Sal, México, and as late as August 25 at Buenos Aires, Durango.

**REMARKS:** The synonymy of *Hyla eximia* has had a varied and confused history. Kel-

logg (1932, p. 164) included *Hyla euphorbiacea* Günther and *Hyla smithii* Boulenger in the synonymy of *eximia*, but he considered *Hyla gracilipes* Cope to be a separate species and having as a synonym *Hyla lafrentzi* Mertens and Wolterstorff. Günther (1901, p. 261) first placed *Hyla gracilipes* in the synonymy of *Hyla eximia*. Taylor (1939b, p. 423) disagreed with Kellogg's recognition of *Hyla gracilipes* and concluded, as did Günther, that *gracilipes* is the same as *eximia*. I have examined the syntypes of *gracilipes* (U.S.N.M. Nos. 15318-15321) and agreed with Taylor that these specimens are representatives of *Hyla eximia*.

Taylor (1939b, p. 426) showed that *Hyla euphorbiacea* Günther was a valid species, distinct from *Hyla eximia*. *Hyla smithii* long has been recognized as a distinct species not closely related to *Hyla eximia*.

Maslin (1957, p. 81) named *Hyla microeximia* from 5 kilometers northwest of Joetepée, Jalisco, México. Duellman (1961e, p. 49) discussed the variation in *Hyla eximia*. A comparison of the holotype of *microeximia* (U.S.N.M. No. 139246) with the syntypes of *Hyla eximia* (U.S.N.M. No. 3248) reveals that the holotype of *microeximia* is larger than either of the two syntypes of *eximia*!

In the foregoing synonymy of *Hyla eximia* I have included three other species for the first time; these are *Hyla cardenasi* Taylor, 1939b; *Hyla wrightorum* Taylor, 1939b; and *Hyla arboricola* Taylor, 1941. Following is a justification of these assignments. The holotype of *Hyla cardenasi* (U.S.N.M. No. 84403) from Puebla, Puebla, México is a gravid female having a snout-vent length of 39 mm. and essentially no dorsal dark markings whatsoever. The comparison of this specimen with a series of *Hyla eximia* and *plicata* reveals that the detailed structure of the hands and feet, especially the amount of webbing on the feet is like that of *eximia* and not of *plicata*. *Hyla eximia* is a rather common frog in the vicinity of Puebla, and I conclude that name *Hyla cardenasi* was based on an unpatterned individual of *Hyla eximia*; dorsal spots are absent in more than 50 per cent of the specimens from the vicinity of Puebla, and dorsal dark stripes are absent in more than 25 per cent of the specimens from that area.

Specimens of *Hyla eximia* from the northern part of the range (Arizona and New Mexico in the United States, and Chihuahua in México) are somewhat larger, more robust, and have proportionately longer legs than do those frogs from the southern part of the range. However, these differences in size and proportions, notwithstanding, the variation in color patterns indicates a very close relationship between the northern and southern populations. Analysis of mating calls of individuals formerly assigned to *Hyla wrightorum* from Apache County, Arizona, with those from throughout the Mexican Plateau, reveal no outstanding differences. The fundamental frequency is slightly higher in those individuals from Apache County, Arizona, than in the other samples, but the range of variation in the former is included in the latter. On the basis of the absence of any distinctive morphological characters and on the basis of general similarity of mating call, I conclude that *Hyla wrightorum* is the same as *Hyla eximia*.

Taylor (1941, p. 118) diagnosed *Hyla arboricola* as different from *eximia* by having a broader head, more webbing on the feet, limbs lacking dark marks, and the absence of a well-defined dark mark on the side of the head. Few adult specimens have been obtained from the highlands of Guerrero, but of these, several have dark markings that are typical of *Hyla eximia*. Furthermore, the proportions of head width and the amount of webbing on the feet fall within the range of variation of *Hyla eximia* on the Mexican Plateau. Unfortunately, recordings of the calls of frogs of the populations in the highlands of Guerrero are not available. Thus, my conclusion that *Hyla arboricola* is a synonym of *eximia* is based solely on morphological evidence, without the benefit of a knowledge of the mating call or the tadpoles of the frogs formerly assigned to *arboricola*.

**ETYMOLOGY:** The specific name is Latin meaning uncommon!

**DISTRIBUTION:** *Hyla eximia* occurs in a variety of upland environments but principally associated with pine forests, in highland areas in central Arizona and New Mexico, in the Huachuca Mountains of southern Arizona, in the Sierra Madre Occidental in northwest-

ern México, and throughout the southern part of the Mexican Plateau, the Sierra Madre Oriental, and Cordillera Volcánica in central México (fig. 250). The species occurs at elevations between 900 and 2900 meters.

See Appendix 1 for the locality records of the 2209 specimens examined.

### *Hyla euphorbiacea* Günther

*Hyla euphorbiacea* Günther, 1859, p. 109 [syn-types, B.M.N.H. No. 1947.2.24.19 from "Cordilleras," México; E. Parzudaki collector; B.M.N.H. Nos. 1947.2.24.15 and 16 from "México," B.M.N.H. No. 1947.2.24.18 from "Cordilleras," México, and B.M.N.H. No. 1947.2.24.17 from Córdoba (Veracruz?), México; Auguste Sallé collector]. Taylor, 1939b, p. 426. Smith and Taylor, 1948, p. 82.

*Hyliola bocourti* Mocquard, 1889b, p. 341 [syn-types, M.N.H.N. Nos. 1266 (2 specimens), 6370 (6 specimens), 6371 (6 specimens) from Alta Verapaz, Guatemala; Marie-Firmin Bocourt collector].

*Hyla bocourti*: Günther, 1901 (1885-1902), p. 263. Stuart, 1963, p. 35.

**DIAGNOSIS:** This moderately small green frog with a brown face mask and brown spots or stripes dorsally has smooth skin, small discs, no webbing between the fingers, and the toes about two-thirds webbed. The presence of small yellow spots on the dark brown posterior surfaces of the thighs immediately distinguishes this species from other members of the *eximia* group. Other Middle American hylids with yellow spots on the posterior surfaces of the thighs include *Hyla pictipes* and *xanthosticta* in Costa Rica; both of those frogs have relatively large discs and have webbing between the fingers.

**DESCRIPTION:** Males of this moderately small species attain a maximum snout-vent length of 29.6 mm., and females reach 40.6 mm. In a series of 25 males from the Valley of Oaxaca, Oaxaca, México, at an elevation of about 1500 meters, the snout-vent length is 31.6 to 37.3 (mean, 34.7) mm.; the ratio of tibia length to snout-vent length is 0.434 to 0.480 (mean, 0.457); the ratio of foot length to snout-vent length is 0.410 to 0.469 (mean, 0.440); the ratio of head length to snout-vent length is 0.270 to 0.304 (mean, 0.287); the ratio of head width to snout-vent length is 0.304 to 0.335 (mean, 0.320), and the ratio of the diameter of the tympanum to that of the eye is 0.548 to 0.733 (mean, 0.629). Five



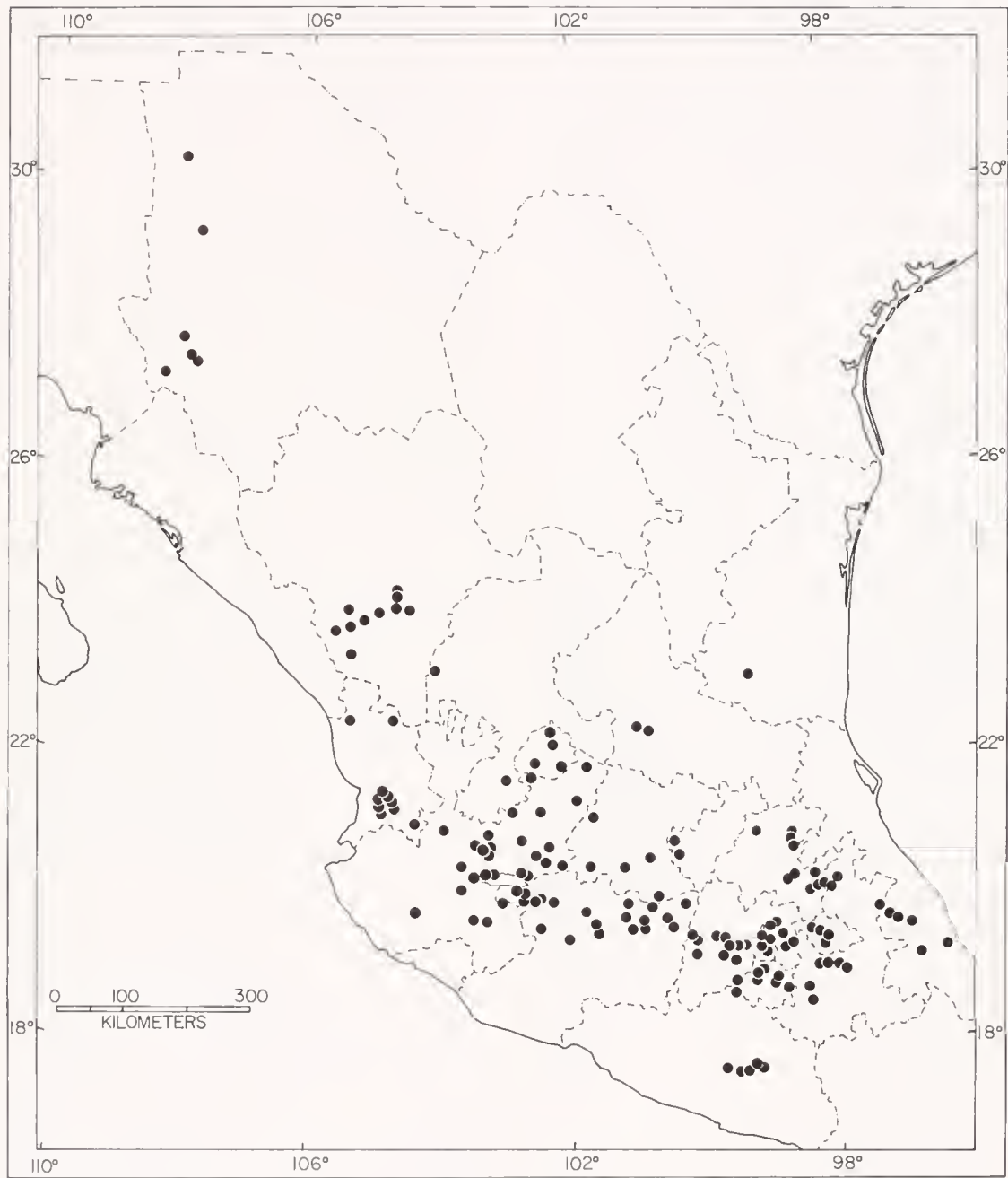


FIG. 250. Distribution of *Hyla eximia*.

females from the same locality have snout-vent lengths of 34.0 to 39.6 (mean, 36.4) mm. and show no significant differences in proportions. In a series of 25 males from Llano de las Flores, Oaxaca, México, at an elevation of 3100 meters, the snout-vent length is 33.3 to 39.6 (mean, 36.6) mm. These slightly larger frogs do not differ from those from the Valley of Oaxaca in proportions, except that the tympanum is proportionately smaller; the ratio of the diameter of the tympanum to that of the eye is 0.472 to 0.658 (mean, 0.570).

The head is slightly narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded, and in lateral profile it is round. The snout is moderately long; the nostrils are barely protuberant at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is barely concave; the lips are thin and barely flared. A moderately thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point behind the angle of the jaw. The fold obscures the upper edge of the tympanum, which otherwise is distinct, and separated from the eye by a distance equal to about one-half the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. An indistinct row of tubercles is present on the ventrolateral edge of the forearm, and a thin dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about three-fifths of the diameter of the tympanum. The subarticular tubercles are large and conical; none is bifid. The supernumerary tubercles are conical and distinct on the proximal segments of the digits. An elevated, usually bifid, palmar tubercle is present. The prepollex is barely enlarged and in breeding males bears a thin horny nuptial excrecence. The webbing between the fingers is vestigial (fig. 243D). The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the tympanum or to the posterior corner of the eye. A thin transverse dermal fold is present on the heel and

a distinct tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is ovoid and elevated. A small conical outer metatarsal tubercle is present. The toes are long and slender and bear discs that are smaller than those on the fingers. The subarticular tubercles are large and round, and the supernumerary tubercles are low, indistinct, and present only on the proximal segments of the digits. The toes are slightly more than one-half webbed (fig. 244D). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the distal end of the antepenultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs; it is covered by a short anal sheath. The skin on the throat, belly, and posteroventral surfaces of the thighs is strongly granular; elsewhere, the skin is smooth. The tongue is cordiform, moderately notched posteriorly, and free behind for about one-third of its length. The denticulous processes of the prevomers are small, posteromedially inclined elevations between the small, ovoid choanae. Males have two to five teeth on each process and a total of five to nine (mean, 7.8) prevomerine teeth; females have three to five teeth on each process and a total of six to ten (mean, 8.1) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla euphorbiacea* is green or pale tan above with or without dark brown dorsal markings (pl. 66, fig. 6). The dorsum varies from pale green and olive-green to pale tan. Usually the dorsum is marked by elongate dark brown streaks or small round brown spots; in approximately 40 per cent of the specimens examined the dorsal markings are absent or reduced to a few small spots posteriorly. A dark brown stripe extends from the snout through the nostril, eye, and tympanum onto the flank, and

usually to the groin. This stripe is bordered above by a narrow white line. The anterior and posterior surfaces of the thighs, the outer edges of the shanks, and the inner edges of the tarsi are orange-brown to black with bright yellow spots. The belly is creamy white. The vocal sac is yellow or brown with creamy yellow spots anteriorly. The iris is pale coppery bronze.

In preservative, the dorsum is pale bluish gray or grayish tan. Dorsal markings are brown. Individuals lacking brown marks on the back usually lack dark transverse marks on the limbs. A distinct white anal stripe is invariably present, and a distinct white stripe on the outer edge of the shank usually is evident. Pale spots are present on the posterior surfaces of the thighs in all specimens; however, in some individuals the spots are absent in the groin and on the anterior surfaces of the thighs.

**TADPOLES:** A typical tadpole in developmental stage 31 has a body length of 11.5 and a total length of 28.0 mm. The body is slightly deeper than wide; in dorsal profile the snout is bluntly rounded, and in lateral profile it is round. The eyes are small, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The spiracle is directed posterodorsally at a point below the midline and about three-fifths the distance from the tip of the snout to the posterior end of the body. The anal tube is long and dextral. The caudal musculature is slender and tapers to the tip of the acutely rounded tail. The caudal fins are deep; at midlength of the tail the depth of the dorsal fin is half again as great as the depth of the caudal musculature. The dorsal fin extends onto the body (fig. 245D).

Tadpoles are pale tan above and pale golden below. The throat is dark gray with silvery flecks. The caudal musculature is tan with faint grayish brown reticulations on the musculature and fins. In preservative, the body and caudal musculature is creamy tan; faint gray flecks and reticulations are evident on the musculature and fins.

The mouth is small and directed anteroventrally. Lateral folds are absent in the lips. The median one-third of the upper lip is bare,

whereas the rest of the lips are bordered by two or three rows of small papillae. The beaks are moderately robust and bear small serrations. The upper beak is in the form of a broad arch with slender lateral processes, and the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and the second upper row is broadly interrupted medially. The first and second lower rows are nearly as long as the upper rows, and the third lower row is noticeably shorter (fig. 246D).

**MATING CALL:** The call of *Hyla euphorbiacea* consists of a short series of quickly repeated, low-pitched notes. An analysis of the calls of 12 individuals recorded at temperatures of 17° to 18°C. from the Valley of Oaxaca show that there are five to ten (mean, 7.4) notes per call group. The note repetition rate is 600 to 900 (mean, 773) notes per minute, and the duration of each note is 0.03 to 0.06 (mean, 0.05) of a second. The call rate is 18 to 39 (mean, 25.5) call groups per minute, and the pulse rate is 100 to 120 (mean, 112) pulses per second. The fundamental frequency varies from 104 to 130 (mean, 114.3) cycles per second and the dominant frequency varies from 2080 to 2736 (mean, 2345.8) cycles per second (pl. 14, fig. 1).

Calls of *Hyla euphorbiacea* have been recorded at temperatures between 12.0°C. and 21.5°C. Analysis of these records indicate that there is little variation in the number of notes per call group, but the note repetition rate, call rate, pulse rate, and the fundamental and dominant frequencies increase at higher temperatures, whereas the duration of the notes decreases at higher temperatures (table 50).

**NATURAL HISTORY:** *Hyla euphorbiacea* is especially ubiquitous in the Valley of Oaxaca, where the frogs call by the thousands from flooded grassy fields after heavy rains in July and August. The frogs also occur at high elevations in pine-oak and pine forest, where they breed in shallow temporary ponds. Males call while sitting in shallow water or while floating on the water and holding onto blades of grass or small sticks. The eggs are laid in loose clumps in grassy parts of the pond. Tadpoles have been found in shallow grassy ponds, a shallow muddy pool in oak forest on



TABLE 50  
Comparison of Certain Parameters of the Mating Calls of  
*Hyla euphorbiacea* at Different Temperatures  
(Means are given in Parentheses.)

Parameter	12.5°C	17-18°C	21.5°C
N	5	12	6
Call Rate (min.)	12-18 (15.0)	18-39 (25.5)	28-36 (31.3)
Note Repetition Rate (min.)	300-466 (368)	600-900 (773)	686-935 (820)
Pulse Rate (sec.)	65-90 (72)	100-120 (112)	100-120 (115)
Fundamental Frequency (cps)	70-87 (81.8)	104-130 (114.3)	104-139 (118.7)
Dominant Frequency (cps)	1653-2175 (1793)	2080-2736 (2346)	2300-2782 (2518)
Duration of Notes (sec.)	0.08-0.11 (0.098)	0.03-0.06 (0.050)	0.04-0.05 (0.047)

Cerro Machín, and in roadside ditches between June 23 and August 31.

In the dry season frogs of this species seek shelter in bromeliads; adults have been taken from bromeliads at Cumbres de Acultzingo, Veracruz, in January and at Llano de las Flores, Oaxaca, in March.

REMARKS: The status of *Hyla bocourti* (Mocquard) is doubtful. The only specimens that have been referred to this species are from the vicinity of Cobán on the Atlantic slopes of the Guatemalan highlands. Three subadults (F.M.N.H. Nos. 20684-20686) have snout-vent lengths of 26.9, 29.8, and 30.6 mm., respectively; an adult female (U.M.M.Z. No. 90870) has a snout-vent length of 39.8 mm. The latter is partially dried, brittle, and formalin burned. This specimen was obtained from a bromeliad at Finca Samac, Alta Verapaz, Guatemala, by Laurence C. Stuart on April 26, 1938. In his field notes, Stuart stated: "Above light brown with slightly darker brown longitudinal streaks—trace of similar colored broad band between eyes—a distinct dark brown streak from nostril to eye and along sides where it widens—sharply demarked above but indistinct below—belly brown mottled with gray—posteriorly and somewhat laterally bright yellow spotted with brown—legs brown above with several darker bars—below light yellow with brown mottling." The three subadults from Cobán all

have dark thighs with pale spots. I am convinced that on the basis of morphology and coloration, *Hyla bocourti* cannot be distinguished from *Hyla euphorbiacea*. The tadpoles and mating calls of the Guatemalan population herein referred to as *euphorbiacea* are unknown; consequently, the possibility does exist that there are biological differences between the two populations. However, at the present time on the basis of the existing knowledge, it seems best to me to consider the Guatemalan and the Oaxacan specimens as examples of one species. Of course, this poses a zoogeographic problem. *Hyla euphorbiacea* is known from elevations in excess of 1500 meters in Oaxaca and at elevations of about 1000 meters on the northern slopes of the highlands in Guatemala. Intervening between the ranges of these two populations are the lowlands of the Isthmus of Tehuantepec and the highlands of Chiapas and Guatemala, which are inhabited by *Hyla walkeri*, a species obviously closely related to, but distinct from, *Hyla eximia*.

ETYMOLOGY: The specific name is derived from the Latin *euphorbea*, referring to plants of the family Euphorbiaceae and the Latin suffix *-aceus*, meaning belonging to.

DISTRIBUTION: *Hyla euphorbiacea* occurs in the Sierra Madre Oriental southward from central Veracruz into Oaxaca, in the Valley of Oaxaca, and in the mountains to the south of

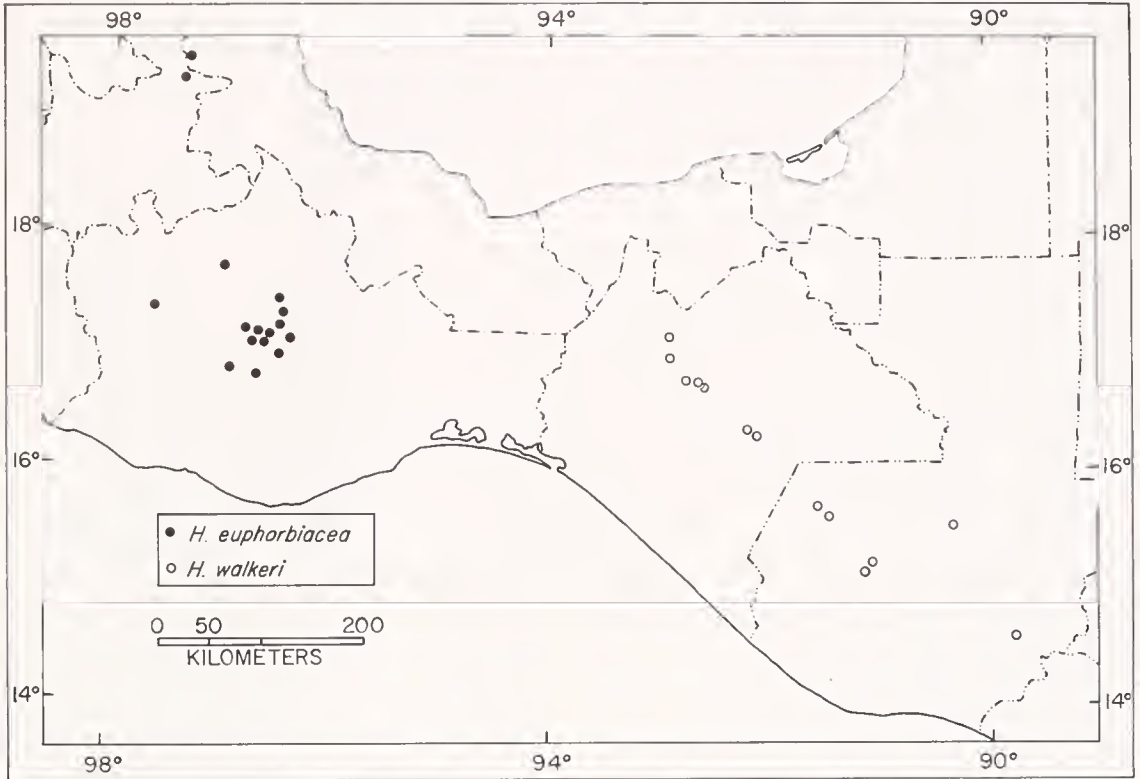


FIG. 251. Distribution of *Hyla euphorbiacea* and *Hyla walkeri*.

the Valley of Oaxaca; in addition, the species is known from the Atlantic slopes of the highlands in Alta Verapaz, Guatemala (fig. 251). In México, the species is known from elevations between 1600 and 3150 meters, and in Guatemala it is known from elevations of about 1000 meters.

See Appendix 1 for the locality records of the 810 specimens examined.

#### *Hyla walkeri* Stuart

*Hyla walkeri* Stuart, 1954b, p. 165 [holotype, U.M.M.Z. No. 106817 from Aserradero San Lorenzo (12 kilometers airline, slightly east of north of Jalapa), Jalapa, Guatemala; Laurence C. Stuart collector]; 1963, p. 37.

*Hyla euphorbiacea biseriata* Lynch, in Smith, Langebartel, and Williams, 1964, p. 24 [*nomen nudum*].

**DIAGNOSIS:** This moderately small species having a green dorsum with a dark brown face mask and usually with a pair of brown lines posteriorly on the dorsum has smooth skin, small discs, no webbing between the

fingers, and the toes about two-thirds webbed. The presence of uniformly tan posterior surfaces of the thighs immediately distinguishes *walkeri* from *euphorbiacea*, which has yellow spots on the thighs. *Hyla regilla* differs by having a dark interorbital triangular mark, and *cadaverina* differs by being brown or gray and having tuberculate skin. Most specimens of *eximia* have transverse bars on the thighs (usually absent in *walkeri*) and have brown spots and/or more extensive stripes on the dorsum. *Hyla plicata* is larger (males to 44 mm.) than *walkeri* (36 mm.) and has slightly more webbing on the feet; the web extends to the base of the penultimate phalanx of the fifth toe in *plicata* and only to the distal end of the antepenultimate phalanx in *walkeri*.

**DESCRIPTION:** Males of this moderately small species attain a maximum snout-vent length of 35.9 mm., and females reach 37.8 mm. In a series of 20 males from 18 kilometers northwest of Comitán, Chiapas, México, the snout-vent length is 29.0 to 35.6 (mean, 32.0)

mm.; the ratio of tibia length to snout-vent length is 0.463 to 0.517 (mean, 0.491); the ratio of foot length to snout-vent length is 0.445 to 0.495 (mean, 0.475); the ratio of head length to snout-vent length is 0.294 to 0.321 (mean, 0.305); the ratio of head width to snout-vent length is 0.308 to 0.361 (mean, 0.332), and the ratio of the diameter of the tympanum to that of the eye is 0.469 to 0.633 (mean, 0.553). Three females from the same locality have snout-vent lengths of 30.8 to 32.6 (mean, 31.6) mm., and do not differ from the males significantly in proportions. Specimens from Guatemala exhibit the same range in measurements and proportions, except that they have slightly smaller tympani. In a series of 40 males from Soloma and San Juan Ixeoy, Departamento Huehuetenango, Guatemala, the ratio of the diameter of the tympanum to that of the eye is 0.444 to 0.552 (mean, 0.497).

The head is slightly narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded, and in lateral profile it is round. The snout is moderately long, and the slightly protuberant nostrils are situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is barely concave; the lips are thick and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and diffuses onto the body above the insertion of the arm. The fold covers the upper edge of the tympanum, and the rest of the tympanic ring is barely discernible. The tympanum is separated from the eye by a distance about two-thirds of the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A row of low, indistinct tubercles is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are small, indistinct, and present only on the proximal segments of the digits. A

small, round palmar tubercle is present. The prepollex is barely enlarged, and in most breeding males does not bear a nuptial excrescence. The webbing on the hand is vestigial (fig. 243E). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A thin transverse dermal fold is present on the heel, and a distinct tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, ovoid, and barely elevated. The outer metatarsal tubercle, if present, is small and subconical. The toes are long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are moderately small and round, and the supernumerary tubercles are low, indistinct, and present only on the proximal segments of the digits. The toes are about one-half webbed (fig. 244E). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs, and a short anal sheath is evident. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is eordiform, shallowly notched behind, and free posteriorly for about one-third of its length. The dentigerous processes of the prevomers are small posteromedially inclined elevations between the posterior margins of the small, ovoid choanae. Males have three to six teeth on each process and a total of six to 11 (mean, 8.2) prevomerine teeth; females have three to six teeth on each process and a total of six to 12 (mean, 8.7) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla walkeri* is bright green or greenish tan above with or without dark brown longitudinal markings



(pl. 66, figs. 4 and 5). Generally the dorsum is green. There is a dark brown line extending from the snout through the nostril and eye to the midflank or groin; this brown stripe is bordered above by a narrow white line. The dorsum is marked by a dorsolateral brown stripe posteriorly, a row of dorsolateral brown spots, or no markings whatsoever. The dorsal surfaces of the thighs usually are uniform green, but in a few specimens brown flecks or small spots are present. The upper lip is flesh-colored on the margin and separated by a narrow brown line from the yellowish green color from the nostril to the angle of the jaw. The posterior surfaces of the thighs are dull yellowish brown. The venter is pale creamy yellow and vocal sac in breeding males is brown anteriorly and yellow posteriorly. The iris is dull bronze with fine black reticulations.

In preservative, the dorsal ground color is pale bluish gray. The dorsal markings are brown; in some individuals these are narrowly outlined with white. The edge of the upper lip, the upper border of the lateral brown stripe, the outer edge of the shank, and the stripe above the anus are white. The posterior surfaces of the thighs are creamy tan, and the venter is creamy white.

**TADPOLES:** A typical tadpole in developmental stage 37 has a body length of 16.0 mm. and a total length of 37.2 mm. The body is deep, slightly deeper than wide; the snout in dorsal profile is bluntly rounded, and in lateral profile it is round. The eyes are small, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point below the midline about two-thirds of the distance from the tip of the snout to the posterior edge of the body. The anal tube is long and dextral. The caudal musculature is moderately slender and tapers gradually to the tip of the acutely pointed tail. The caudal fins are moderately deep; at midlength of the tail, the depth of the dorsal fin is slightly greater than the depth of the caudal musculature. The dorsal fin extends onto the body (fig. 245E).

The tadpoles are dark brown above with a silvery iridescence on the venter. The cau-

dal musculature is creamy tan with dark brown or grayish brown mottling and reticulations on the musculature and fins. In preservative, the body is dark brown; the caudal musculature is tan and there is a heavy concentration of dark pigment on the dorsal aspects of the musculature.

The mouth is moderately small and directed anteroventrally. Lateral folds are absent from the lips. The median half of the upper lip is bare; the rest of the lip is bordered by two rows of small papillae. The beaks are massive and bear short, blunt serrations. The upper beak is in the form of a broad arch with long, slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are long, and the second upper row is broadly interrupted medially. The first and second lower rows are about equal in length, but much shorter than the upper rows. The first lower row is narrowly interrupted medially in some specimens. The first lower row is noticeably shorter (fig. 246E).

**MATING CALL:** The call of *Hyla walkeri* consists of groups of four to six short, quickly repeated, low-pitched notes. The call rate varies from 30 to 48 (mean, 38.0) call groups per minute, and the note repetition rate varies from 960 to 1200 (mean, 1090) notes per minute. The duration of the note varies from 0.03 to 0.04 (mean, 0.035) of a second, and the pulse rate is about 120 pulses per second. The fundamental frequency varies from 135 to 184 (mean, 158) cycles per second, and the dominant frequency varies from 1755 to 2175 (mean, 1910) cycles per second (pl. 14, fig. 2).

**NATURAL HISTORY:** *Hyla walkeri* inhabits pine-fir and pine-oak forests. In the rainy season, males call from temporary grassy ponds, frequently in clearing or meadows. The males call while floating on the water with their hind limbs partly flexed or with the hands grasping grass or debris. Some individuals were observed sitting in shallow water near the shore. All clasping pairs were observed floating in the water. Stuart (1954b, p. 168) reported this species calling on June 17-18, 1952, at San Lorenzo, Departamento Jalapa, Guatemala. In June, 1960, I obtained

calling males from 10 to 18 kilometers northwest of Comitán, Chiapas, México. Porter (1962, p. 168) reported males calling from a meadow at San Cristóbal de las Casas, Chiapas, México, on June 15, 1960. At the same locality, I found adults in rotting pine logs on February 17, 1961.

Tadpoles were obtained from grassy ponds at 10 kilometers northwest of Comitán, Chiapas, on June 17, 1960; tadpoles and metamorphosing young were obtained at a grassy pond at 2.5 kilometers south of Jitotal, Chiapas on August 5, 1960.

REMARKS: In most features of its morphology, *Hyla walkeri* is indistinguishable from *Hyla eximia* and *euphorbiacea*. In coloration, it differs from both of these by generally lacking transverse marks on the dorsal surfaces of the thighs. From *euphorbiacea* it differs by lacking the yellow spots in the groin and on the anterior and posterior surfaces of the thighs. The calls of *Hyla walkeri* and *euphorbiacea* are alike in consisting of short groups of notes; in this respect, the calls of both of these species differ from *eximia*, the call of which consists of individual notes not grouped together.

ETYMOLOGY: The specific name is a patronym for Charles F. Walker.

DISTRIBUTION: *Hyla walkeri* occurs in the central highlands of Chiapas, México, the Sierra de los Cuchumatanes in western Guatemala, and on the plateaus of central Guatemala, and in the highlands of southeastern Guatemala (fig. 251). The species is known from elevations between 1450 and 2340 meters.

See Appendix 1 for the locality records of the 194 specimens examined.

#### The *Hyla versicolor* Group

DEFINITION: The frogs in this group are medium-sized species having a tan, gray, or green dorsum with darker irregular blotches or spots; the limbs are barred. The venter is white; the vocal sac is gray, and the palpebral membrane is clear. The flanks and anterior and posterior surfaces of the thighs are uniformly pale or mottled with black or dark brown. The dorsum is moderately rugose. The fingers are barely webbed, and the feet

are one-half to two-thirds webbed. A strong tarsal fold is present, but an axillary membrane and dermal appendages on the limbs are absent. Males have a single, median, subgular vocal sac and horny nuptial excrescences on the prepollices. The skull is only moderately ossified, and a large frontoparietal fontanelle is present (fig. 252). The sphenethmoid is not ossified anteriorly, and the nasals are large and not, or barely, separated medially. The squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends no more than half of the distance to the maxillary. The columella is moderately expanded distally. A quadratojugal is present and articulates with the maxillary. The prevomers are moderately well ossified and bear teeth. The medial ramus of the pterygoid does not articulate with the prootic. The tadpoles have moderately deep fins and anteroventral mouths with two upper and three lower rows of teeth. The mating calls consist of a rattling series of short notes or distinct short, pulsed notes. The haploid number of chromosomes is 12.

COMPOSITION: Five species (*arenicolor*, *avivoca*, *chrysoscelis*, *femoralis*, and *versicolor*) comprise the group, which is widespread in North America east of the Sierra Nevada and the Colorado Desert. Only *Hyla arenicolor* occurs in México; of that species, 599 preserved frogs from México have been examined. Three lots of tadpoles and eleven skeletons from the United States have been examined.

COMMENTS: Blair ("1958" [1959]) defined

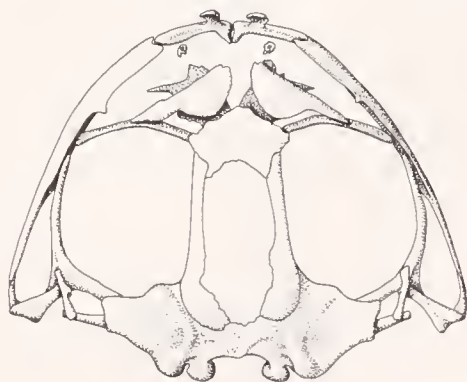


FIG. 252. Dorsal view of the skull of *Hyla arenicolor*, K.U. No. 44441.  $\times 4$ .

the *versicolor* group on the basis of call structure to include *arenicolor*, *phaeocrypta* (= *avivoca*), *femoralis*, *versicolor*, and *baudinii*. Starrett (1960b) and Duellman and Trueb (1966) showed that *baudinii* belonged in *Smilisca*. The group was modified by Johnson (1966) who showed that "*versicolor*" was comprised of two cryptic species, *chrysoscelis* and *versicolor*, differing from one another by mating calls and a high degree of hybrid inviability.

Members of the *versicolor* group are very much alike in size, structure, and coloration, except *femoralis*, which is smaller than the other species and has relatively smooth skin and bold markings on the anterior and posterior surfaces of the thighs. According to Blair ("1958" [1959]) the call of *femoralis* is most like that of *arenicolor*, the only species occurring in Middle America.

On the basis of structure of the adults and tadpoles and on the nature of the mating calls the *Hyla versicolor* group seems to be most closely related to the *Hyla cinerea* group of southeastern North America. The *versicolor* group apparently is not closely related to any of the groups endemic to México and Central America.

### *Hyla arenicolor* Cope

*Hyla affinis* Baird, 1854, p. 61 [syntypes, U.S.N.M. No. 11410 (originally 3261) (five specimens) from "northern Sonora," México (type locality restricted to Santa Rita Mountains, Arizona, by Smith and Taylor (1950, p. 354) and further restricted to Peña Blanca Springs, 10 miles northwest of Nogales, Santa Cruz County, Arizona, by Gorman (1960, p. 218), who designated U.S.N.M. No. 11410a as the lectotype); John H. Clark collector; preoccupied by *Hyla affinis* Spix, 1824, from Brasil]. Brocchi, 1881, p. 43.

*Hyla arenicolor* Cope, 1886a, p. 84 [replacement name for *Hyla affinis* Baird, 1854, preoccupied by *Hyla affinis* Spix, 1824]. Boulenger, 1882a, p. 373.

*Hyla copii* Boulenger, 1887, p. 53 [syntypes, B.M.N.H. Nos. 1947.2.23.26 and 27 from El Paso, Texas, U.S.A.; Alphonso Forrer collector]. Günther, 1901 (1885-1902), p. 266.

*Hyla coper* Cope, 1888, p. 80 [typographical error for *copii*].

*Hyliola digueti* Mocquard, 1889a, p. 165 [syntypes, M.N.H.N. No. 492 (five specimens) from Territory of Tepic, México (restricted to Tepic, Nayarit, México, by Smith and Taylor, 1950); León Diguet collector].

*Hyla arenicolor* (part): Kellogg, 1932, p. 156. Smith and Taylor, 1948, p. 89.

**DIAGNOSIS:** This medium-sized species has tuberculate skin, vestigial webbing on the hands, and a dull gray or brown dorsum marked with irregular darker spots or blotches. The posterior surfaces of the thighs are dull yellow or tan, and numerous white flecks are present in the anal region. *Hyla arenicolor* resembles *cadaverina*, which differs by having slightly more webbing, smaller discs, fewer and less distinct supernumerary tubercles, and smaller tympanum; the diameter of the tympanum is about half of the diameter of the eye in *cadaverina* and about two-thirds of the diameter of the eye in *arenicolor*. Other Middle American hylids that might be confused with *arenicolor* all have webbing between the fingers.

**DESCRIPTION:** Males of this medium-sized species attain a maximum known snout-vent length of 51.2 mm., and females reach 57.1 mm. In a series of 22 males from the vicinity of Guadalajara, Jalisco, México, the snout-vent length is 32.8 to 39.5 (mean, 35.5) mm.; the ratio of tibia length to snout-vent length is 0.454 to 0.518 (mean, 0.489); the ratio of foot length to snout-vent length is 0.385 to 0.442 (mean, 0.413); the ratio of head length to snout-vent length is 0.301 to 0.360 (mean, 0.327); the ratio of head width to snout-vent length is 0.354 to 0.398 (mean, 0.377), and the ratio of the diameter of the tympanum to that of the eye is 0.543 to 0.730 (mean, 0.652). Three females from the same area have snout-vent lengths of 39.5 to 44.4 (mean, 41.6) mm. The size of the specimens from the vicinity of Guadalajara is typical over most of the Mexican Plateau. Duellman (1961, p. 46) noted that specimens from higher elevations in Michoacán were smaller than those from lower elevations; seven males from elevations above 1400 meters have snout-vent lengths of 32.3 to 38.4 (mean, 34.7) mm., whereas nine males from elevations below 1400 meters have snout-vent lengths of 44.7 to 51.2 (mean, 49.1) mm. Thirteen males from the vicinity of Chilpancingo, Guerrero, have snout-vent lengths of 44.7 to 48.9 (mean, 45.7) mm. In northern México, the frogs are somewhat larger than they are on the plateau in the southern part of the range; for example, the largest of 36 males from Chihuahua has a snout-vent length of 42.8 mm. It seems as



though there is a general trend from north to south on the Mexican Plateau for a decrease in size, but that individuals from lower elevations in the southern part of the range are by far the largest of the species. There appears to be no significant variation in proportions.

The head is as wide as the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded, and in lateral profile it is bluntly rounded. The snout is short, and the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is barely concave; the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point just posterior to the angles of the jaw. In some individuals the fold obscures the upper edge of the tympanum, but in most specimens, the tympanum is entirely distinct, situated posteroventral to the eye, and separated from the eye by a distance equal to about half of the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A row of distinct or partially fused tubercles is present on the ventrolateral edge of the forearm and a weak transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about half of the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercle on the fourth finger usually is bifid. Moderately large supernumerary tubercles and a large elliptical palmar tubercle are present. The prepollex is moderately enlarged and in breeding males lacks a horny nuptial exerescence. The webbing is vestigial (fig. 253A). The hind limbs are moderately short and robust; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to a point between the eye and nostril. A thin transverse dermal fold is present on the heel, and an elevated, flap-like tarsal fold extends the full length of the tarsus. Numerous small tubercles are present on the plantar surface of the tarsus. The inner metatarsal tubercle is moderately large, ele-

vated, and elliptical. A conical outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are about equal in size to those on the fingers. The toes are about one-half webbed (fig. 253B). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs. The skin on the dorsum is moderately tuberculate; small tubercles are present on the dorsal surfaces of the limbs. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere, on the venter, the skin is smooth. The tongue is narrowly cordiform, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are short, postero-medially inclined, narrowly separated medially elevations between the moderately small, ovoid choanae. Males have four to six teeth on each process and a total of nine to 12 (mean, 10.4) prevomerine teeth; females have five to seven teeth on each process and a total of 10 to 13 (mean, 11.4) prevomerine teeth. The vocal slits extend a short distance posterolaterally from the midlateral base of the tongue. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla arenicolor* is dull grayish brown with darker brown or gray spots (pl. 64, fig. 2). The typical coloration of an individual from Agua del Obispo, Guerrero, México, in life is grayish brown above with dark brown spots and faint transverse bands on the limbs. The groin, anterior and posterior surfaces of the thighs, and ventral surfaces of the hind limbs is orange-yellow. The belly is white, and the vocal sac is purplish brown. The eye is grayish copper. Individuals found by day frequently are quite pallid by comparison with those found at night. For example, an individual found in

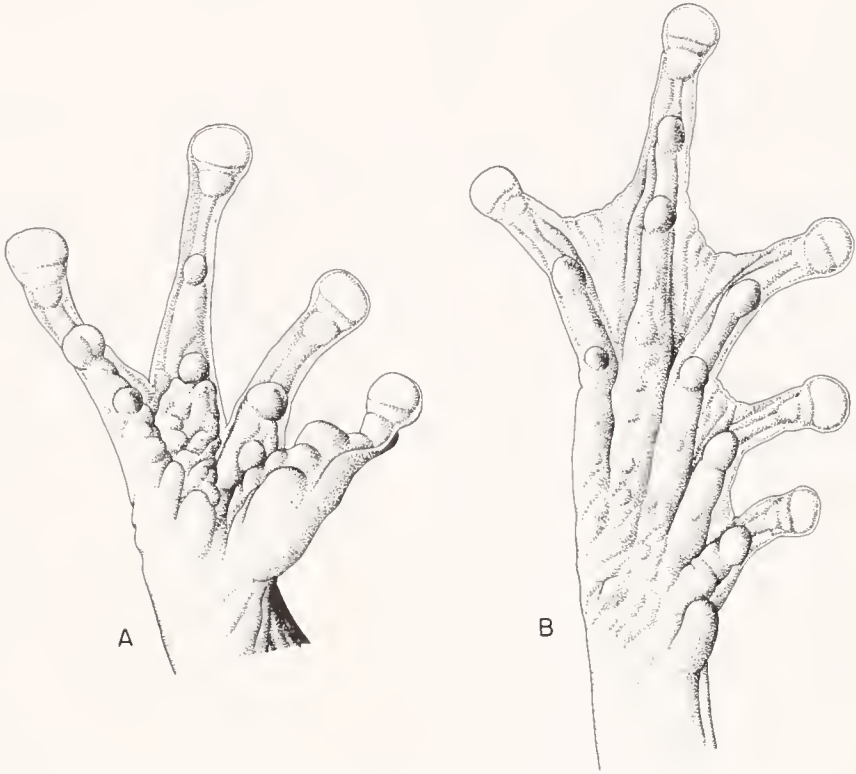


FIG. 253. Hand (A) and foot (B) of *Hyla arenicolor*, K.U. No. 86935.  $\times 4$ .

a shady ravine at Chinapa, Michoacán, México, was pale ashy gray (pl. 64, fig. 3).

In preservative, the dorsum varies from tan to dull brown or gray. Numerous spots or small blotches, frequently outlined with black flecks are evident on the dorsum in most individuals. In some specimens, the dark spots are present on the flanks, but in most individuals the flanks are dull gray or brown with minute white flecks. Two to four transverse bands are present on the thighs and shank, and usually two transverse bands are present on the forearm. The posterior surfaces of the thighs are faintly mottled in some individuals from the Mexican Plateau, and in all specimens numerous white flecks are present in the anal region. The throat in breeding males is gray, brown, or black, frequently marked by small white flecks. The throat in some females is faintly spotted with brown.

**TADPOLES:** Zweifel (1961) thoroughly described the tadpoles of this species from the Chiricahua Mountains, Cochise County, Arizona. I am unaware of any tadpoles of *Hyla*

*arenicolor* from México; consequently, the following description is based on Zweifel's material from Arizona.

A typical tadpole in developmental stage 37 has a body length of 12.5 mm. and a total length of 31.9 mm. The body is ovoid, no wider than deep. The dorsal profile of the snout is bluntly rounded, and in lateral profile the snout slopes gradually from the nostrils to the tip. The eyes are large, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is at a point below the midline at about midlength of the body. The anal tube is short and dextral. The caudal musculature is moderately robust and extends nearly to the tip of the bluntly pointed tail. The caudal fins are moderately deep. At midlength of the tail, the depth of the dorsal fin is approximately equal to the depth of the caudal musculature. The dorsal fin does not extend onto the body (fig. 254).

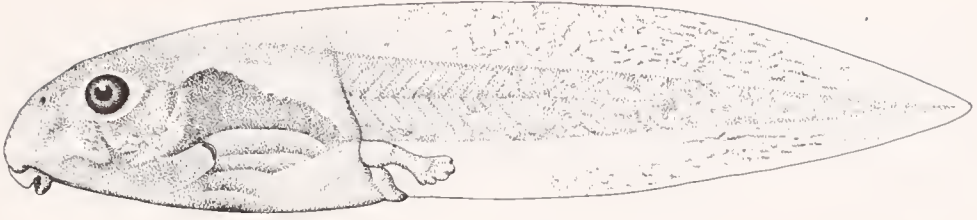


FIG. 254. Tadpole of *Hyla arenicolor*, A.M.N.H. No. 64678.  $\times 4$ .

The mouth is of medium size and in a ventral position. Distinct lateral folds are absent. The median part of the upper lip is bare; the rest of the upper lip is bordered by a single row of small papillae, and the lower lip is fringed by two rows of papillae. Additional small papillae are present laterally in the mouth. The beaks are robust and bear short blunt serrations; the upper beak is in the form of a massive arch with short slender lateral processes, and the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and extend to the margins of the lips, whereas the three lower rows are equal in length, but noticeably shorter than the upper rows. The second upper row is narrowly interrupted medially in all specimens, and the first upper and first lower rows are narrowly interrupted in some individuals (fig. 255).

Zweifel (1961, p. 11) described the coloration of large tadpoles (stages 36 and 41) as being golden brown with no pattern evident on the body but a patchy distribution of superficial xanthophores on the caudal musculature, which gives a mottled appearance to

the tail. He stated that the ventral surfaces are "dense silver (with a golden sheen when seen at the right angle) which gives way abruptly to a golden brown of the dorsum about midway up the side of the body." In preservative, the dorsal part of the body is dull brown and the venter is transparent. The caudal musculature is creamy tan with a concentration of dark brown pigment on the dorsal edge of the musculature and forming faint spots posteriorly. The fins are transparent and marked by fine black flecks or reticulations.

**MATING CALL:** The call of *Hyla arenicolor* consists of a series of short, nasal notes "ah-ah-ah-ah." Some individuals call constantly for two or more minutes. An analysis of the calls of four individuals from the Chiricahua Mountains, Cochise County, Arizona, reveals that the note repetition rate varies from 30 to 38 (mean, 33) notes per minute; the duration of the notes is 0.56 to 0.80 (mean, 0.65) of a second and the pulse rate is 28 to 33 (mean, 29) pulses per second. The fundamental frequency varies from 94 to 113 (mean, 102) cycles per second and the dominant frequency varies from 2112 to 2460 (mean, 2329) cycles per second (pl. 12, fig. 3). An analysis of seven recordings obtained in the Peloncillo Mountains, New Mexico, shows that the frogs there differ slightly by having a slower repetition rate, shorter duration of notes, and a slower pulse rate. The frogs produced 26 to 32 (mean, 27) notes per minute having a duration of 0.53 to 0.75 (mean, 0.64) of a second and 22 to 25 (mean, 24) pulses per second. Two individuals recorded at Amayuca, Morelos, México, produced 64 and 68 notes per minute, and the duration of the notes in each was approximately 0.50 of a second.

**NATURAL HISTORY:** *Hyla arenicolor* inhab-

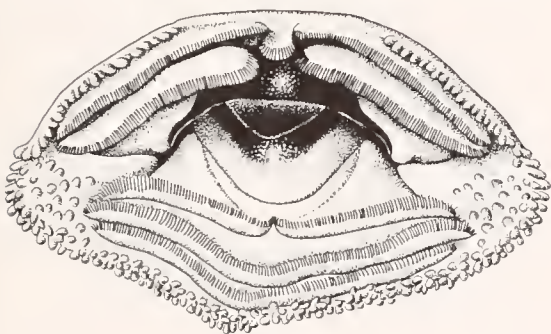


FIG. 255. Mouth of tadpole of *Hyla arenicolor* A.M.N.H. No. 64678.  $\times 20$ .



its a variety of vegetational formations. It occurs over a large part of the Mexican Plateau, where it is found in mesquite-grassland and scrub forest. In the mountains rising from and bordering the Mexican Plateau, this species occurs in pine and oak forest, and on the lower slopes of the highlands the frog occurs in scrub oak and dense thorn forest. However, throughout its range it is always closely associated with small rocky streams; *Hyla arenicolor* inhabits ravines and canyons.

Males call from rocks or occasionally low bushes surrounding quiet pools in canyons. A few males have been observed to call from shallow water in the pools. Calling males have been found from June 25 to July 20 in the vicinity of Barranca del Cobre, Chihuahua, México. Calling males have been obtained on the Mexican Plateau in the vicinity of Guadalajara, Jalisco, between May 25 and July 10, at Lombardia, Michoacán, on July 12, and at Agua del Obispo, Guerrero, on June 19. Zweifel (1961, p. 16) noted the presence of tadpoles in the South Fork of Cave Creek in the Chiricahua Mountains, Cochise County, Arizona, on June 22, 1958 and surmised that breeding must have commenced at least a month earlier. He also found that the species bred at that locality in July.

Zweifel (1961, p. 17) reported egg laying in pools in a canyon on July 12 or 13, 1960 and noted that the period from oviposition to metamorphosis was probably between 50 and 60 days. He gave the snout-vent length of newly metamorphosed young as about 15 mm.

REMARKS: Kellogg (1932, p. 156) provided a thorough discussion of the synonymy of this species. Most references to *Hyla arenicolor* in México (see Kellogg 1932, and Smith and Taylor 1948) concern not only *Hyla arenicolor* but also *Hyla cadaverina*, a species distinguished from *arenicolor* by Gorman (1960) who named it *Hyla californiae*.

The nature of the variation in size and call structure in this species remains unsettled; Jack R. Pierce of Austin College is currently investigating inter-populational variation in this species.

*Hyla arenicolor* is the disjunct southwestern representative of the *Hyla versicolor* group; its present distribution probably is a result of continuous more favorable habitats

during pluvial periods of the Pleistocene or the post-Wisconsin time and its ability to survive in moist pockets in canyons in otherwise highly unfavorable environments.

ETYMOLOGY: The specific name is derived from the Latin *arena*, meaning sand and the Latin *color*, meaning color, and refers to the dull brown dorsal ground color of this species.

DISTRIBUTION: *Hyla arenicolor* occurs in mountainous areas and on high plateaus from southern Utah and Colorado southward to include the eastern two-thirds of Arizona, New Mexico, and west Texas in the United States and the Mexican Plateau and associated mountain ranges, southward to Michoacán, Guerrero, and western Oaxaca (fig. 256). The species occurs at elevations between 300 and 3000 meters.

See Appendix 1 for the locality records of the 599 specimens examined.

#### Genus *Ptychohyla* Taylor

*Ptychohyla* Taylor, 1944a, p. 41 [type species, *Ptychohyla adipoventris* Taylor, 1944a = *Hyla leonhardschultzei* Ahl, 1934]. Smith and Taylor, 1948, p. 91. Stuart, 1963, p. 40. Duellman, 1963c, p. 314.

GENEROTYPE: *Hyla leonhardschultzei* Ahl, 1934. Taylor (1944a, p. 41) proposed the generic name *Ptychohyla* for a new species, *Ptychohyla adipoventris*, described in the same paper (p. 41). Duellman (1960c) compared the holotype of *P. adipoventris* with that of *Hyla leonhardschultzei* and concluded that they were representative of the same species.

ETYMOLOGY: The generic name is derived from the Greek *ptycho*, meaning layer of plate, and *Hylas*, a character in Greek mythology. The generic name is in reference to the plate-like ventrolateral glands characteristic of this genus.

DEFINITION: Frogs of the genus *Ptychohyla* are small to medium in size and have a uniform green or brown dorsum or one that is marked by darker blotches. The flanks are uniform white or marked by black spots, and the venter is white or yellow, with or without spots. The iris is a deep bronze, copper, or red. The palpebral membrane is unmarked. The hands are about one-third webbed or have only a vestige of a web between the fin-

gers. The toes are about two-thirds to three-fourths webbed. Breeding males are characterized by a pair of thickened, pigmented ventrolateral glands, which are usually more distinct in preserved than in living specimens. Breeding males of some species have nuptial excrescences. The vocal sac is single, median, and subgular. The skull is broad, flat, and

has a large frontoparietal fontanelle. The sphenethmoid is wide and broadly attached to the elongate, rather slender nasals, which are separated medially and lie parallel to the maxillaries. The anterior arm of the squamosal is short and extends less than half the distance to the maxillary. The quadratojugal usually is reduced to a small spine-shaped

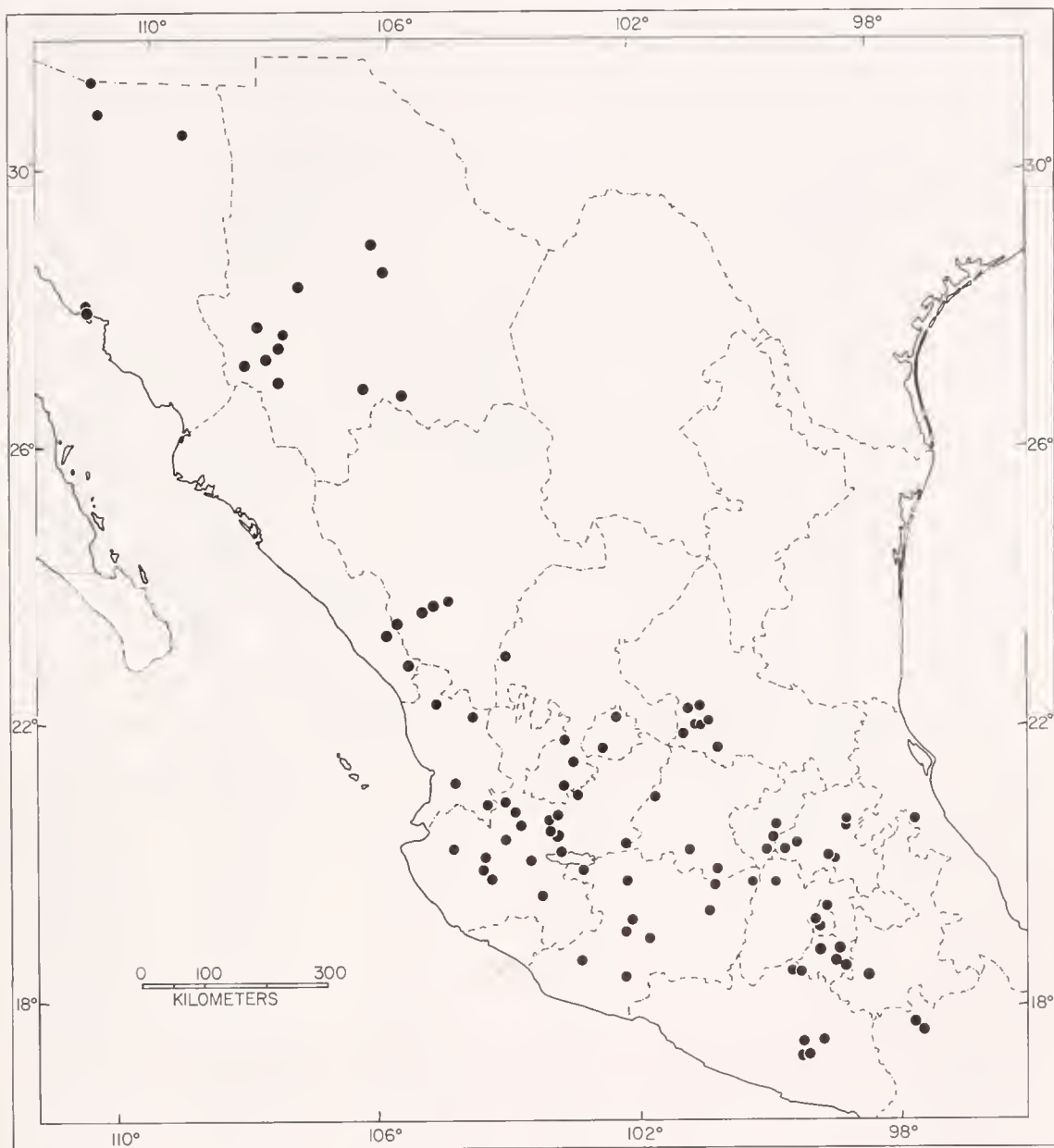


FIG. 256. Distribution of *Hyla arenicolor* in México.

element posteriorly that does not articulate with the maxillary. Teeth are present on the premaxillaries, maxillaries, and prevomers, but are absent from the palatines and parasphenoid. The teeth are simple, elongate, and conical. The teeth on the premaxillary and anterior part of the maxillary are longer, pointed, and terminally curved backwards; whereas posteriorly on the maxillary the teeth become progressively shorter and blunter. The tadpoles are adapted to live in mountain streams; they have stream-lined bodies and long tails bearing low fins. The mouth is large and directed ventrally. There are three upper and three lower rows of teeth in a funnel-shaped mouth in the members of one species group and minimally four upper and six lower rows of teeth in a broad marginate mouth in the members of a second group. The mating calls consist of a series of short notes or a single long note. The haploid number of chromosomes is 12, and the diploid number is 24 (known in *P. ignicolor* and *leonhardschultzei*).

COMPOSITION OF THE GENUS: Five species are currently recognized; two are polytypic, each containing two subspecies. All known species occur only in Middle America. Of the five species, 404 preserved frogs, 13 skeletons, 57 lots of tadpoles, and one preserved clutch of eggs were examined.

ANALYSIS OF CHARACTERS: The largest species is *Ptychohyla euthysanota*; the largest specimen examined is a female of the nominate subspecies having a snout-vent length of 53.3 mm. Members of the *schmidtorum* group (*ignicolor* and *schmidtorum*) are notably smaller; the largest male is 32.8 mm. and the largest female, 38.0 mm. In all species the females are 10 to 15 per cent longer than the males. Few differences in proportions exist between the species (table 51), but certain morphological characters are consistently different between species. A vertical fleshy rostral keel is present in *leonhardschultzei* and *spinipollex* but lacking in the other species. These two species, plus *euthysanota* have the fingers about one-third webbed, a nuptial excrescence consisting of a cluster of spines, and a weak tarsal fold (figs. 257 and 258). *Ptychohyla ignicolor* and *schmidtorum* lack a tarsal fold and nuptial excrescences and have only vestigial webbing between the fingers. The ventrolateral glands distinctive of breeding males are not readily visible in living individuals of *ignicolor* and *schmidtorum*, but in preservative they show as distinctive orange-tan areas. The glands are more distinct in *euthysanota*; in some of these the glands are elevated above the surface of the surrounding skin. The extent of the glands is variable (fig. 259), but some of the varia-

TABLE 51  
Comparison of Sizes and Proportions, with Means in Parentheses,  
of Males of the Taxa of *Ptychohyla*.

Taxon	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Tympanum/ Eye
<i>P. s. schmidtorum</i> .....	25	29.0-32.8 (31.0)	0.453-0.524 (0.481)	0.371-0.409 (0.319)	0.515-0.593 (0.547)
<i>P. s. chamulae</i> .....	40	26.3-30.5 (28.0)	0.460-0.519 (0.482)	0.386-0.429 (0.404)	0.482-0.656 (0.549)
<i>P. ignicolor</i> .....	38	26.6-30.9 (28.1)	0.458-0.496 (0.481)	0.380-0.429 (0.406)	0.366-0.531 (0.429)
<i>P. e. euthysanota</i> .....	17	28.9-38.1 (35.0)	0.444-0.550 (0.487)	0.349-0.405 (0.380)	0.486-0.638 (0.563)
<i>P. e. macrotympaum</i> .....	5	32.0-38.0 (34.9)	0.488-0.520 (0.502)	0.405-0.424 (0.417)	0.500-0.571 (0.541)
<i>P. leonhardschultzei</i> .....	36	28.5-35.6 (31.9)	0.472-0.544 (0.512)	0.386-0.453 (0.420)	0.447-0.619 (0.515)
<i>P. spinipollex</i> .....	32	29.0-41.0 (37.1)	0.469-0.531 (0.490)	0.388-0.426 (0.408)	0.450-0.552 (0.495)



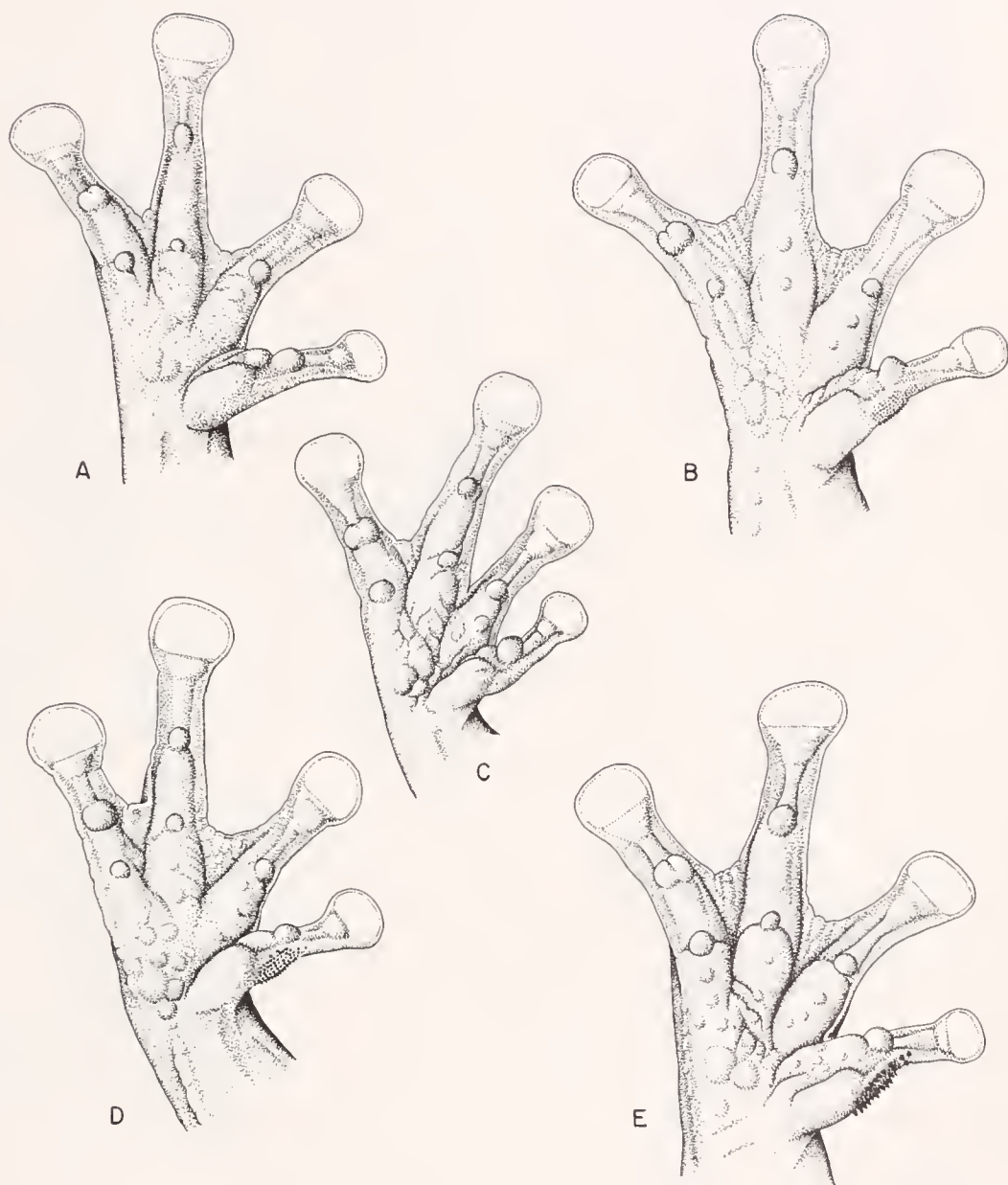


FIG. 257. Hands of the species of *Ptychohyla*. A. *P. schmidtorum schmidtorum*, K.U. No. 58037. B. *P. euthysanota euthysanota*, K.U. No. 58010. C. *P. ignicolor*, K.U. No. 87153. D. *P. leonhard-schultzei*, K.U. No. 101049. E. *P. spinipollex*, K.U. No. 58057.  $\times 6$ .



FIG. 258. Feet of the species of *Ptychohyla*. A. *P. schmidtorum schmidtorum*, K.U. No. 58037. B. *P. cuthysanota cuthysanota*, K.U. No. 58010. C. *P. ignicolor*, K.U. No. 87153. D. *P. leonhardschultzei*, K.U. No. 101049. E. *P. spinipollex*, K.U. No. 58057.  $\times 6$ .

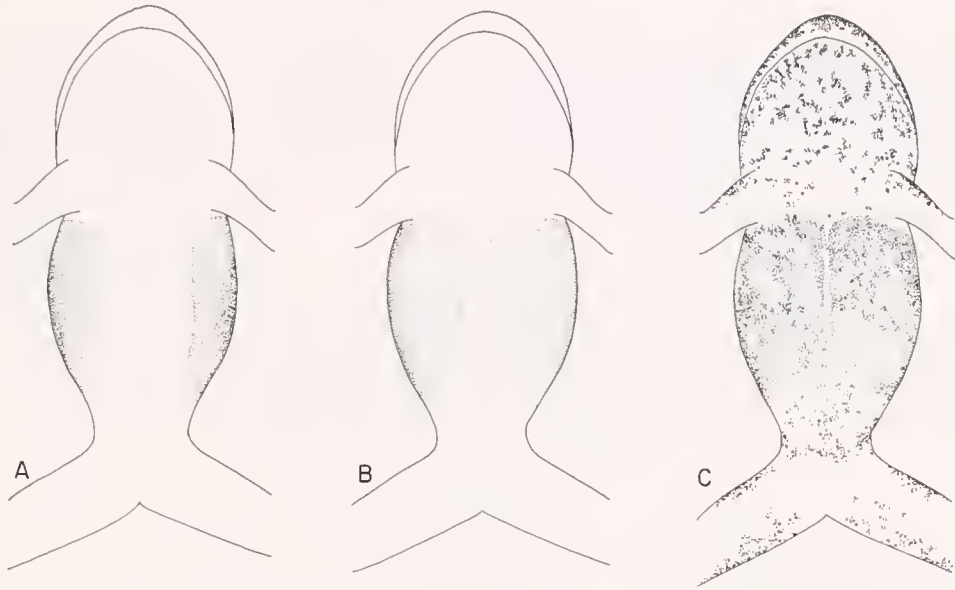


FIG. 259. Extent of ventrolateral glands in three species of *Ptychohyla*. A. *P. euthysanota* *euthysanota*, K.U. No. 58009. B. *P. schmidtorum* *schmidtorum*, K.U. No. 58033. C. *P. ignicolor*, K.U. No. 87158.  $\times 2$ . Note the chin gland and pigmentation in *P. ignicolor*.

tion probably is due to different degrees of development in individual frogs rather than to interspecific differences. Most specimens of *P. ignicolor* and some of *P. schmidtorum* *chamulae* have a small, round glandular area on the chin.

The dorsum is green in *ignicolor* and *chamulae*; in the other species the dorsum is brown, reddish brown, or olive-brown with or without darker blotches or reticulation. The venter and flanks are boldly spotted with black in *leonhardschultzei* and *spinipollex*; the venter is weakly spotted in *euthysanota* and immaculate in *schmidtorum* whereas small flecks are present in *ignicolor*. The anterior and posterior surfaces of the thighs are brown or orange-brown, except in *ignicolor*, which has red or orange-red surfaces of the thighs. *Ptychohyla euthysanota* and *schmidtorum* have a white labial stripe that is continuous onto the flank, and all species have a pale transverse stripe above the anus and white or cream stripes along the outer edges of the forearm and tarsus (pl. 67).

The tadpoles of *ignicolor* and *schmidtorum* have large funnel-shaped mouths; the teeth are arranged in short rows, three above and three below the beaks, which have long, pointed serrations but lack lateral processes.

The tadpoles of *euthysanota*, *leonhardschultzei*, and *spinipollex* have large mouths with a lateral fold and two rows of labial papillae; the teeth are arranged in long rows, four above and six below the beaks, which have short, peg-like serrations and long lateral processes (figs. 260 and 261).

The skulls of the various species are nearly alike, except that the quadratojugal-maxillary arch is always incomplete in *euthysanota*, *ignicolor*, and *schmidtorum*, whereas in some specimens of *leonhardschultzei* and *spinipollex* the arch is complete (fig. 262). Furthermore, the premaxillaries are longer and bear more teeth in *ignicolor* and *schmidtorum* than in the other species.

The mating calls of *ignicolor* and *schmidtorum* consist of a series of short notes and differ from one another in that the notes are shorter, more slowly pulsed, but higher pitched in *schmidtorum*. The calls of *euthysanota*, *leonhardschultzei*, and *spinipollex* consist of one long note and differ in duration, pulse rate, and pitch (table 52, pls. 30 and 31).

**DISTRIBUTION:** The combined distributions of the five species of *Ptychohyla* include the Atlantic and Pacific slopes of the highlands of nuclear Central America and southern Méx-





FIG. 260. Tadpoles of the species of *Ptychohyla*. A. *P. schmidtorum schmidtorum*, K.U. No. 60051. B. *P. ignicolor*, K.U. No. 87637. C. *P. euthysanota euthysanota*, K.U. No. 60042. D. *P. leonhardschultzei*, K.U. No. 104198. E. *P. spinipollex*, K.U. No. 68563.  $\times 12$ .

ico. The range on the Pacific slopes is from central Guerrero to El Salvador and on the Atlantic slopes from northern Oaxaca to north-central Nicaragua. The species of *Ptychohyla* inhabit cloud forests at elevations from 350 to 2200 meters; their discontinuous distribution reflects their dependence upon mountain streams that offer suitable breeding sites.

DISCUSSION: On the basis of the morphological characters of adults and tadpoles and of the mating calls, the species of *Ptychohyla* form two species groups. The *P. schmidtorum* group, containing *schmidtorum* and *ignicolor*, apparently is closer to the generic parental stock than is the *P. euthysanota* group, containing *euthysanota*, *leonhardschultzei*, and *spinipollex*. Duellman (1963c) suggested

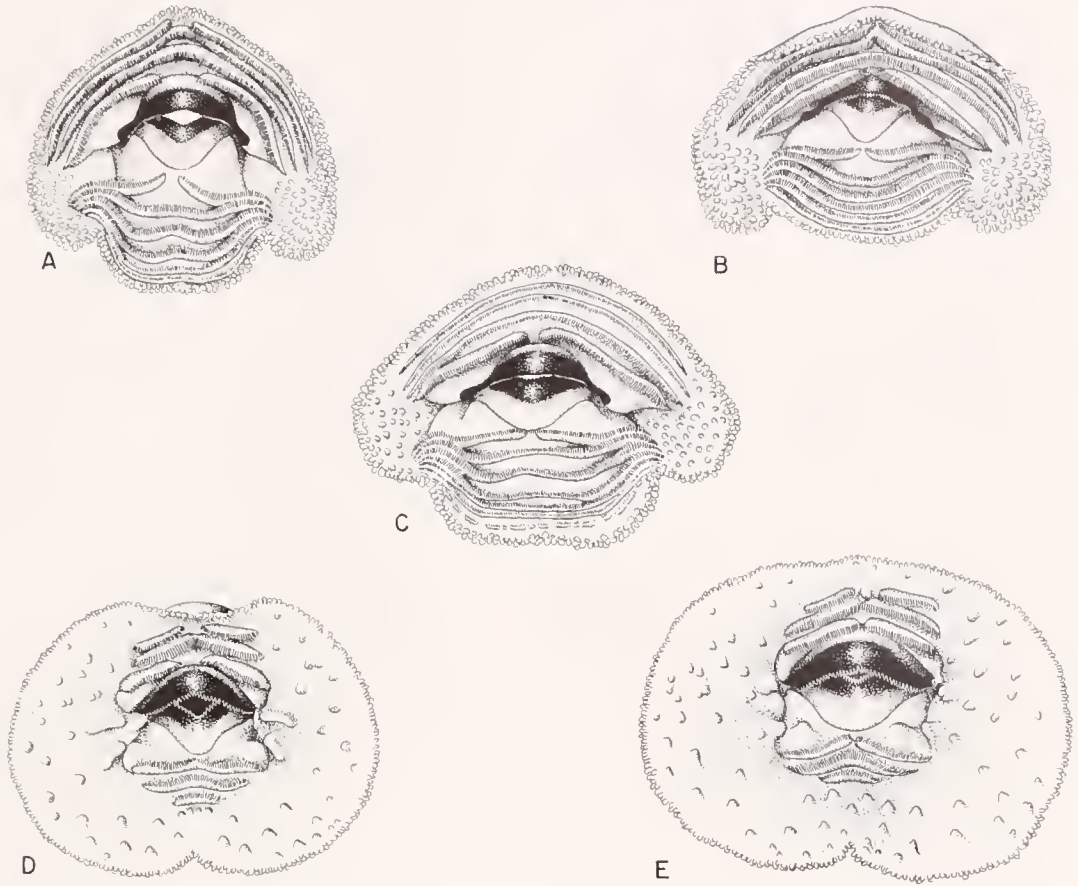


FIG. 261. Mouthparts of tadpoles of the species of *Ptychohyla*. A. *P. euthysanota euthysanota*, K.U. No. 60042. B. *P. leonhardschultzei*, K.U. No. 104198. C. *P. spinipollex*, K.U. No. 68563.  $\times 12$ . D. *P. schmidtorum schmidtorum*, K.U. No. 60051. E. *P. ignicolor*, K.U. No. 87637.

that *Ptychohyla* had evolved from a stock which gave rise to the *Hyla uranochroa* group in lower Central America.

Only the presence of ventrolateral glands in breeding males singularly distinguished *Ptychohyla* from *Hyla*. Although such a criterion is tantamount to dissent by some museum taxonomists, the character apparently is indicative of monophyletic origin of the five species. The generic recognition thus has a phylogenetic basis, as well as being a matter of convenience.

Possibly *Ptychohyla euthysanota* and *schmidtorum* differentiated from a common ancestor through selection for larval characteristics. The resulting differences in the adaptations of the tadpoles (riffles in *euthysanota* and pools in streams in *schmidtorum*)

was enhanced by differences in the mating calls (see Duellman, 1963e, for discussions of ecological segregation and interspecific relationships).

*Ptychohyla spinipollex* and *leonhardschultzei* seem to be more closely related to one another than either is to *euthysanota*. Probably a stock of *euthysanota* was isolated on the Atlantic slopes of northern Central America from *euthysanota* on the southern slopes. The frogs on the Atlantic slope differentiated and spread into the mountains of Oaxaca, where through isolation by the barrier of the Isthmus of Tehuantepec they developed into *leonhardschultzei*, while the stock on the Atlantic slopes of Central America evolved into *spinipollex*. Probably subsequent to the differentiation of *leonhard-*

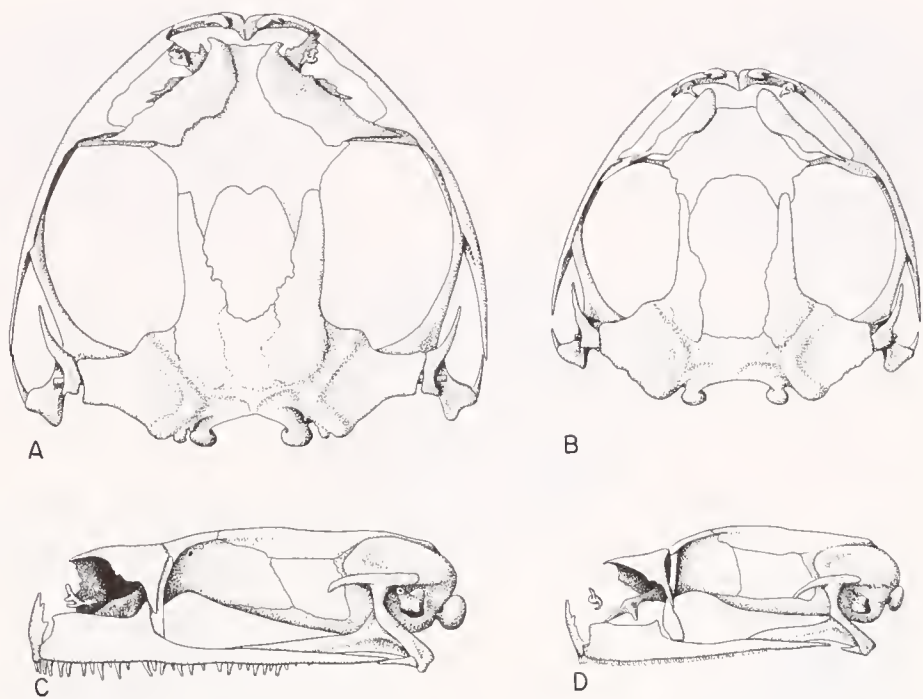


FIG. 262. Skulls of *Ptychohyla*. A and C. *P. spinipollex*, K.U. No. 59939. B and D. *P. ignicolor*, K.U. No. 103034.  $\times 5$ .

TABLE 52

Characteristics of the Mating Calls, with Means in Parentheses, of the Species *Ptychohyla*.

Species	N	Notes per Call Group	Duration of Note (seconds)	Pulses per Second	Dominant Frequency (cps)
<i>P. schmidtorum</i> .....	6	8-9 (8.5)	0.054-0.070 (0.064)	96-121 (110)	3350-3450 (3400)
<i>P. ignicolor</i> ... ..	2	11-13 (12)	0.078-0.080 (0.079)	123-129 (126)	3100-3200 (3150)
<i>P. euthysanota</i> .....	7	1	0.60-0.65 (0.62)	91-102 (95.3)	3000-3200 (3070)
<i>P. leonhardschultzei</i> .....	2	1	0.62-0.95 (0.79)	76-78 (77)	2700-2800 (2750)
<i>P. spinipollex</i> .. ..	1	1	0.46	147	4300



*schultzei* and *spinipollex* from *euthysanota* and during a time of cooler more equable climate than exists now, *euthysanota* and *schmidtorum* invaded the Central Highlands of Chiapas. Subsequent climatic changes isolated populations of each in the Central Highlands, where *euthysanota macrotympanum* and *schmidtorum chamulae* evolved. *Ptychohyla ignicolor* apparently represents a stock of *schmidtorum* that crossed the Isthmus of Tehuantepec and became isolated in Oaxaca on the western side of the isthmus.

### *Ptychohyla schmidtorum* Stuart

*Ptychohyla schmidtorum* Stuart, 1954b, p. 169 [holotype, F.M.N.H. No. 27055 from El Porvenir (17 kilometers airline west of San Marcos), Departamento San Marcos, Guatemala; Karl P. Schmidt collector].

**DIAGNOSIS:** This species is distinguished from other *Ptychohyla* by lacking a tarsal fold and spinous nuptial excrescences on the thumb in breeding males, and by having only a vestige of web between the fingers and a relatively large tympanum, the diameter of which is more than half the diameter of the eye. The internarial area is depressed, and the toes are about three-fourths webbed. A white lateral stripe is usually present, and the thighs are creamy tan or pale brown. See the diagnoses and descriptions of the subspecies for further comparisons.

**CONTENT:** Two subspecies are recognized: *Ptychohyla s. schmidtorum* Stuart inhabits the Pacific slopes from extreme eastern Oaxaca to southwestern Guatemala and *P. schmidtorum chamulae* Duellman occurs on the Atlantic slopes of the Central Highlands of Chiapas.

Minor differences in the number of premerine teeth and in proportions exist between the subspecies, which are readily distinguished by differences in color. *Ptychohyla s. schmidtorum* has a brown dorsum, a white suborbital spot, and in life a red iris, whereas *P. schmidtorum chamulae* has a green dorsum, no suborbital spot, and in life a reddish bronze iris.

**DISTRIBUTION:** *Ptychohyla schmidtorum* occurs at elevations of 350 to 2200 meters on the Atlantic slopes of the Central Highlands of Chiapas, México, and on the Pacific slopes

of the Sierra Madre from eastern Oaxaca, México to western Guatemala (fig. 263).

### *Ptychohyla schmidtorum schmidtorum* Stuart

*Ptychohyla schmidtorum* Stuart, 1954b, p. 169 [holotype, F.M.N.H. No. 27055 from El Porvenir (17 kilometers airline west of San Marcos), Departamento San Marcos, Guatemala; Karl P. Schmidt collector]; 1963, p. 41.

*Ptychohyla schmidtorum schmidtorum*: Duellman, 1963c, p. 331.

**DIAGNOSIS:** This small subspecies of *Ptychohyla* can be distinguished from other members of the genus by its lack of a tarsal fold, nuptial spines in breeding males, and extensive webbing on the hand. The brown dorsum, white lateral stripe, and suborbital white spot also distinguish this subspecies from other *Ptychohyla*. The coloration of *P. s. schmidtorum* is nearly identical to that of the Costa Rican *Hyla rufoculis*, which lacks the ventrolateral glands in breeding males.

**DESCRIPTION:** This is a moderately small, slender species; males attain a maximum snout-vent length of 32.8 mm. (mean, 25 specimens from Finca La Paz, Departamento San Marcos, Guatemala, 31.0 mm.), and females reach 38.3 mm. (mean, 9 specimens, 34.9 mm.). In the sample of 25 males from Finca La Paz, the ratio of tibia length to snout-vent length is 0.453 to 0.524 (mean, 0.481); the ratio of foot length to snout-vent length is 0.371 to 0.409 (mean, 0.391); the ratio of head length to snout-vent length is 0.309 to 0.326 (mean, 0.320); the ratio of head width to snout-vent length is 0.303 to 0.319 (mean, 0.311), and the ratio of the diameter of the tympanum to that of the eye is 0.515 to 0.593 (mean, 0.547). Too few specimens are available from other parts of the range to determine the presence of geographic variation in size and proportions.

The head is no wider than the body, and the top of the head is flat or slightly convex. In dorsal profile the snout is narrowed, but truncate; in lateral profile the snout is rounded above and truncate. The snout is moderately long; the nostrils are barely protuberant and are situated about three-fourths the distance from the eyes to the tip of the snout. The internarial area is depressed. The canthus is rounded, but distinct; the loreal re-

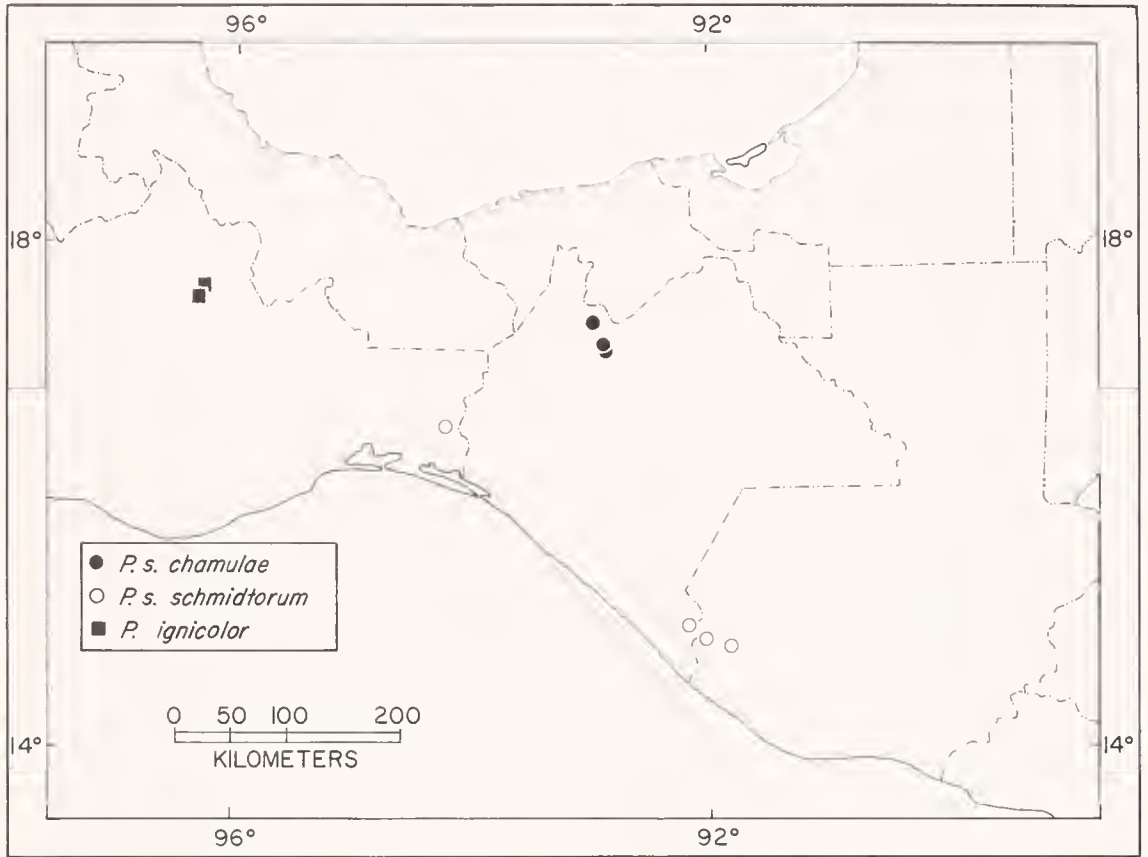


FIG. 263. Distribution of the members of the *Ptychohyla schmidtorum* group.

gion is barely concave, and the lips are thin and barely flared. A moderately heavy dermal fold extends from the posterior corner of the eye above the tympanum and curves downward to the insertion of the arm; the fold obscures the upper part of the tympanum, which otherwise is distinct. The tympanum is posteroventral to the eye and is separated from the eye by a distance equal to the diameter of the tympanum.

The arm is moderately long and not noticeably robust; no axillary membrane is present. A thin dermal fold extends along the outer edge of the forearm and onto the base of the fourth finger; a transverse dermal fold is present on the wrist. The fingers are moderately short and robust; the diameter of the disc of the third finger is equal to the diameter of the tympanum. The subarticular tubercles are rather small and subconical; the

distal tubercle on the fourth finger is bifid in most specimens. Supernumerary tubercles are either lacking or few in number and quite indistinct. The prepollex is moderately enlarged; and in breeding males a nuptial exerescence is lacking. Two small palmar tubercles are present. The webbing between the fingers is vestigial (fig. 257A). Webbing is lacking between the first and second fingers and barely evident between the others. The hind limbs are relatively short; the adpressed heels barely overlap. The tibiotarsal articulation extends to the posterior corner of the eye. The tarsal fold is absent. The inner metatarsal tubercle is low, flat, ovoid, and not visible from above. The outer metatarsal tubercle is minute, round and present in only about one-half of the specimens. The toes are moderately long and bear discs that are nearly as large as those on the fingers. The

subarticular tubercles are moderately large and subconical. Small, indistinct supernumerary tubercles are present on the basal segments of the third, fourth, and fifth toes in some specimens. The toes are about three-fourths webbed (fig. 258A). The webbing connects the first and second toes at the level of the base of the penultimate phalanges; the webbing continues from the middle of the penultimate phalanx of the second toe to the distal end of the antepenultimate phalanx of the third toe. The web extends from the base of the disc of the third toe to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the level of the upper edges of the thighs. The anal sheath is broad and moderately heavy, although not long. The anal region is covered by moderately large tubercles. The skin on the dorsum and ventral surfaces of the legs is smooth; that on the throat, belly, and posteroventral surfaces of the thighs is granular. In breeding males the ventrolateral glands extend nearly from the axilla to the groin and are only narrowly separated medially. In most specimens the tongue is ovoid and marginate, but in four individuals the tongue is shallowly notched behind and in three others the tongue is eordiform. The tongue is only slightly free posteriorly. Males have five to 11 (mean, 6.2) and females, seven to 11 (mean, 8.7) prevomerine teeth situated on small triangular elevations between the ovoid inner nares. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Ptychohyla schmidtorum schmidtorum* is reddish brown with indistinct darker brown markings (pl. 67, fig. 1). The dorsal markings consist of small irregular blotches that are interconnected. The limbs are marked by irregular and indistinct brown transverse bands; usually there are three or four bands on the forearm, thigh, and shank, and two or three bands on the tarsus. The third and fourth fingers and the outer three toes are brown; the first and second fingers and the first and second toes are orange-yellow. The posterior surfaces of the

thighs are pale reddish tan; the webbing on the feet is yellowish tan. A narrow white labial stripe is expanded to form a distinct suborbital spot. The labial stripe continues over the base of the forearm. This is continuous with a broad creamy white lateral stripe that extends to the groin. A narrow creamy white stripe is present on the ventrolateral edges of the forearm and tarsus. An enamel white stripe is present on the heel and above the anus. The belly is white; the ventrolateral glands are creamy white. The iris is red.

In preservative the dorsum is reddish brown with indistinct darker brown markings. The first and second fingers are creamy white, and the third and fourth fingers are brown. The dorsal surfaces of the tarsi and third, fourth, and fifth toes are tan with brown spots; the first and second toes and the webbing on the feet is creamy tan. The enamel white stripes are evident in all preserved specimens. The ventral surfaces of the hind limbs and the anterior and posterior surfaces of the thighs are creamy tan. The belly is white and unspotted; the ventrolateral glands are pale brown.

Some individuals when active at night, had a pale brown dorsum with dull olive-green markings. Otherwise, there is no noticeable variation in coloration.

**TADPOLES:** A typical tadpole in developmental stage 28 from Finca La Paz, Departamento San Marcos, Guatemala, has a total length of 36.0 mm. and a body length of 10.6 mm. The body is slightly wider than deep and only slightly depressed. In dorsal profile the body is ovoid and widest just posterior to the eyes. In lateral profile the snout is rounded; the mouth is directed ventrally. The eyes are small and directed dorso-laterally; the nostrils are barely protuberant and are directed anteriorly from a position about midway between the eyes and the snout. The spiracle is sinistral and situated posteroventrally to the eye. The anal tube is dextral. The tail is long and slender; the caudal musculature is robust. The fins are shallow; the dorsal fin barely extends onto the body and is deepest at a point about two-thirds the length of the tail. The ventral fin has an even depth throughout most of its



length. The tip of the tail is pointed (fig. 260A).

The body is mottled brown and creamy gray above and below; the mouth is colored like the body. The caudal musculature is creamy tan, and the caudal fin is transparent. A dark brown streak is present mid-laterally on the anterior one-third of the caudal musculature; the rest of the tail and all of the caudal fin are heavily flecked with brown. The eye is red in life.

The mouth is large; the thin, fleshy lips are greatly expanded and form a large, funnel-shaped disc. The width of the mouth is equal to about two-thirds the greatest width of the body. The outer edges of the lips have one row of small papillae. The inner surfaces of the mouth are smooth except for scattered large papillae. The beaks are robust; the upper beak forms a broad arch and lacks lateral processes. Both beaks have moderately long, pointed serrations. There are three upper and three lower rows of teeth. All rows are short. The first and third upper rows in most of the specimens, and the first lower row in some specimens, are interrupted medially. The upper rows are approximately equal in length, whereas the lower rows decrease in length from the first to the third (fig. 261D).

**MATING CALL:** The call of *Ptychohyla s. schmidtorum* consists of a series of short, raucous low-pitched notes. The complete call usually consists of one short series of notes alternating with two long series. The numbers of notes per series in one individual, seemingly having a typical call, were 5-8-8-3-9-9. The duration of each note is approximately 0.065 seconds, and the pulse rate is 96 to 119 pulses per second. The dominant frequency is about 3400 cycles per second, (pl. 30, fig. 1).

**NATURAL HISTORY:** *Ptychohyla s. schmidtorum* inhabits cloud forest. The species breeds in clear mountain streams where the males call from vegetation along the stream. The tadpoles live in pools in the mountain streams. There they adhere to small pebbles and stones in the relatively quiet water. Two metamorphosing young have snout-vent lengths of 14.2 and 14.6 mm. These speci-

mens were obtained at Finca La Pas, Departamento San Marcos, Guatemala, in late July. Four metamorphosing young obtained at the same locality by Dr. L. C. Stuart on May 6, 1949 completed their metamorphosis on May 10, at which time they had snout-vent lengths of 15.5 to 17.0 (mean, 16.1) mm.

**REMARKS:** Lynch and Smith (1966) recorded four specimens of *Ptychohyla schmidtorum chamulae* from the Sierra Madre above Zanatepec, Oaxaca, México. They stated that the specimens agreed with the original description of that subspecies (Duellman, 1961b) and did not differ from an individual from "20 mi. N. Jitotal, Chiapas, Mexico." I have examined the four specimens from the Sierra Madre (U.I.M.N.H. Nos. 56187-56190) and their comparative specimen from North of Jitotal (U.I.M.N.H. No. 57002). The latter specimen is in relatively good condition and certainly is an example of the subspecies *chamulae*. The four specimens from the Sierra Madre are formalin burned, so that it is not possible to determine what the color was in life. Since there are no notes on the coloration of the living frogs and since the specimens are from the Pacific slopes of the Sierra Madre, it is most reasonable to assume that they are representative of *P. s. schmidtorum*.

There is no evidence for the integration between *Ptychohyla schmidtorum schmidtorum* and *chamulae*. The ranges of the subspecies are separated by the interior depression of the Chiapas. Nonetheless, the striking similarities in the morphological characters of the adults and of the tadpoles, combined with the nearly identical mating calls strongly suggest that the populations on the Atlantic slopes of the Central Highlands of Chiapas are conspecific with the populations on the Pacific versant of the Sierra Madre.

**ETYMOLOGY:** The subspecific name is a patronym for Karl P. and Franklin J. W. Schmidt, in honor of their extensive collections made in southern Guatemala.

**DISTRIBUTION:** *Ptychohyla schmidtorum schmidtorum* inhabits cloud forests at elevations between 1300 and 2200 meters on the Pacific slopes of the Sierra Madre from eastern Oaxaca, México, southeastward to western Guatemala (fig. 263).

See Appendix 1 for the locality records of the 52 specimens examined.

***Ptychohyla schmidtorum chamulae* Duellman**

*Ptychohyla chamulae* Duellman, 1961b, p. 354 [holotype, K.U. No. 58063 from a stream above (6.2 kilometers by road south of) Rayón Mescalapa, Chiapas, México, elevation 1690 meters; William E. Duellman, Dale L. Hoyt, and John Wellman collectors].

*Ptychohyla schmidtorum chamulae* Duellman, 1963c, p. 334.

**DIAGNOSIS:** This small subspecies of *Ptychohyla* can be distinguished from other members of the genus by its lack of a tarsal fold, nuptial spines in breeding males, extensive webbing on the hand, and red flash-colors on the thighs. The dorsum is green, and a white lateral stripe usually is present. The only other green *Ptychohyla* is *ignicolor*, which lacks a white lateral stripe and has red or orange flash colors. The coloration of *P. schmidtorum chamulae* resembles that of the Costa Rican and Panamanian *Hyla uranochroa*, which differs by having a yellow venter and in lacking ventrolateral glands.

**DESCRIPTION:** This is a small, slender frog; males attain a maximum snout-vent length of 30.5 mm. (mean, 40 specimens from streams south of Rayón Mescalapa, Chiapas, México, 28.0 mm.), and females reach 31.8 mm. (mean, 4 specimens, 30.8 mm.). In this sample of 40 males, the ratio of tibia length to snout-vent length is 0.460 to 0.519 (mean, 0.482); the ratio of foot length to snout-vent length is 0.386 to 0.429 (mean, 0.404); the ratio of head length to snout-vent length is 0.309 to 0.357 (mean, 0.332); the ratio of head width to snout-vent length is 0.305 to 0.346 (mean, 0.322), and the ratio of the diameter of the tympanum to that of the eye is 0.482 to 0.656 (mean, 0.549). Since all specimens are from a few localities in one small area there is no basis for a discussion of geographic variation.

Structurally *Ptychohyla schmidtorum chamulae* is like the nominate subspecies; the reader is referred to the account of *Ptychohyla schmidtorum schmidtorum* for a detailed description.

The general coloration of *Ptychohyla schmidtorum chamulae* is bright green with a white lateral stripe (pl. 67, fig. 2). The

dorsal surfaces of the head, body, and limbs are bright green. The first and second fingers are pale orange. A thin white labial stripe is expanded to form a spot below the eye. This white stripe continues over the forearm and along the side of the body. In most specimens, this stripe continues onto the flanks and to the groin, but in a few the stripe terminates above the forearm, and in some it terminates at mid-flank. In two specimens the lateral stripe is absent. The anterior and posterior surfaces of the thighs are yellowish brown and the webbing of the feet is dull brown. A narrow white stripe is present on the ventrolateral edge of the forearm and on the ventrolateral edge of the tarsus and foot. An enamel white stripe is present on the heel and above the anus. The belly is deep yellow, and the ventrolateral bands are pale orange. The iris is reddish bronze.

In preservative the dorsum is reddish brown with dark purplish brown markings on the back and shanks. The first finger is creamy tan, and the other fingers are pale brown. The dorsal surfaces of the tarsi, third, fourth, and fifth toes are dull tan with brown spots. The first and second toes are creamy tan, and the webbing on the feet is brown. The anterior and posterior surfaces of the thighs are tan. The white stripes are evident. The throat and chest are white, and the belly and ventral surfaces of the limbs are cream. A few brown flecks are present on the belly in most specimens. The ventrolateral glands are orange-tan.

All specimens were uniform green above when found at night; later some changed to pale green on the dorsum with irregular yellowish tan blotches. Most males have brown flecks on the throat and on the ventrolateral glands, but some specimens are immaculate below, and one has dark brown mottling on the throat.

**TADPOLES:** A typical tadpole in developmental stage 27 has a total length of 37.3 mm. and a body length of 12.0 mm. The structure of the body and the mouth is like that of the nominate subspecies. The body is dark brown above and dark gray below; the fleshy part of the mouth is creamy gray mottled with dark brown. The caudal musculature is pale tan with a heavy suffusion of brown flecks;

the caudal fin is transparent with brown flecks; a dark brown streak is present mid-laterally on the anterior one-fifth of the caudal musculature and is bordered below by a cream-colored spot. The eye is brown in life.

**MATING CALL:** The call of *Ptychohyla schmidtorum chamulae* is nearly indistinguishable from that of the nominate subspecies. The call consists of a series of short notes, three to nine notes per series. The duration of each note is 0.054 to 0.070 seconds. There are 96 to 110 pulses per second, and the dominant frequency varies from 3350 to 3450 cycles per second.

**NATURAL HISTORY:** This species inhabits cascading mountain streams in the cloud forests on the northern slopes of the Central Highlands of Chiapas. Tadpoles were found in quiet pools in the streams, where they adhere to pebbles and small stones on the bottom. The smallest known tadpole has a total length of 17.2 mm. and has only three upper and two lower rows of teeth. At a stream 6.2 kilometers south of Rayón Mes-calapa, Chiapas, metamorphosing young were found on June 16 and August 5. Each of two completely metamorphosed young have a snout-vent length of 15.7 mm. Another having a snout-vent length of 16.2 mm., has a tail stub 2 mm. in length and a completely metamorphosed mouth. Two others have snout-vent lengths of 13.6 and 14.4 mm. and tail lengths of 11.5 and 8.1 mm., respectively; in these specimens the mouth parts are incompletely metamorphosed.

The lack of intergrades between *Ptychohyla s. schmidtorum* and *chamulae* is discussed in the account of the nominate subspecies. The four specimens from the Sierra Madre above Zanatepec, Oaxaca, México, reported by Lynch and Smith (1966) as being examples of this subspecies are considered by me to be specimens of *P. s. schmidtorum* (see account of nominate subspecies).

**ETYMOLOGY:** The trivial name *chamulae* is derived from Chamula, the name of the Indian tribe inhabiting the region where this subspecies occurs.

**DISTRIBUTION:** *Ptychohyla schmidtorum chamulae* is known from several localities between Jitotol and Soluschiapa, Chiapas, México, on the northern slopes of the Central

Highlands between elevations of 350 and 1700 meters (fig. 263).

See Appendix I for the locality records of the 77 specimens examined.

### *Ptychohyla ignicolor* Duellman

*Ptychohyla ignicolor* Duellman, 1961b:352 [holotype, U.M.M.Z. No. 119603 from 6 kilometers (by road) south of Campamento Vista Hermosa, Oaxaca, México; Thomas E. Moore collector]; 1963c, p. 337.

**DIAGNOSIS:** This small species of *Ptychohyla* lacks a tarsal fold, nuptial spines in breeding males, and extensive webbing on the hand. The dorsum is green, and the venter is flecked with black. The anterior and posterior surfaces of the thighs are red, orange, or orange-brown. Labial and lateral stripes are absent. The only other *Ptychohyla* having a green dorsum is *P. schmidtorum chamulae*, which has a lateral white stripe and creamy tan anterior and posterior surfaces of the thighs.

**DESCRIPTION:** In this small, slender species the males attain a maximum snout-vent length of 30.9 mm. (mean, 38 specimens from the vicinity of Campamento Vista Hermosa, Oaxaca, México, 28.1 mm.), and females reach 33.1 mm. (mean, 7 specimens, 32.1 mm.). In the sample of 38 males the ratio of tibia length to snout-vent length is 0.458 to 0.496 (mean, 0.481); the ratio of foot length to snout-vent length is 0.380 to 0.429 (mean, 0.406); the ratio of head length to snout-vent length is 0.298 to 0.350 (mean, 0.331); the ratio of head width to snout-vent length is 0.315 to 0.366 (mean, 0.346), and the ratio of the diameter of the tympanum to that of the eye is 0.366 to 0.531 (mean, 0.429). All known specimens are from the vicinity of Campamento Vista Hermosa.

The head is as wide as the body; the top of the head is flat. In dorsal profile the snout is bluntly rounded; in lateral profile the snout is truncate. The snout is relatively long; the nostrils are barely protuberant and are situated about four-fifths the distance from the eyes to the tip of the snout. The canthus is slightly elevated and rounded; the loreal region is distinctly concave, and the lips are moderately thick and flared. A thin dermal fold extends from the posterior corner of the eye above the tympanum to the angle of the



jaws. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arm is moderately long and slender; no axillary membrane is present. A faint row of tubercles is present on the outer edge of the forearm, and an indistinct transverse fold is present on the wrist. The fingers are short and broad and bear moderately large discs; the disc on the third finger is slightly larger than the diameter of the tympanum. The subarticular tubercles are moderately large and round; the distal tubercle on the fourth finger is bifid in most specimens. Supernumerary tubercles are either absent or present as a few indistinct elevations on the proximal segments of the third and fourth fingers. An irregularly shaped, small palmar tubercle is present. The prepollex is slightly enlarged, and in breeding males nuptial excreseences are lacking. The fingers have only a trace of webbing (fig. 257C). The hind limbs are rather short and slender; the adpressed heels barely overlap. The tibiotarsal articulation extends to the anterior corner of the eye. No tarsal fold is present. The inner metatarsal tubercle is small, flat, and elliptical; it is barely visible from above. The toes are moderately long, but robust. The subarticular tubercles are moderately large and round; supernumerary tubercles, if present, are small and indistinct. The discs are nearly as large as those on the fingers. The toes are about three-fourths webbed (fig. 258C). The web extends from the base of the penultimate phalanx of the first toe to the middle of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs; a short, thin anal flap is present. A pair of large tubercles is present below the anal opening, and small tubercles are present ventral to lateral to the large ones. The skin on the dorsum and

ventral surfaces of the limbs is smooth; that on the throat, belly, and posteroventral surfaces of the thighs is granular. The ventrolateral glands in breeding males are noticeably thickened and extend from the axilla nearly to the groin; in some specimens the glands meet midventrally on the chest. A round, thickened gland is present on the anterior part of the chin. The tongue is ovoid or cordiform, shallowly notched behind or marginate, and only slightly free posteriorly. There are three to nine (mean, 6.1) prevomerine teeth in males and four to ten (mean, 7.3) in females. The teeth are situated on rounded elevations between the slightly larger, round choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Ptychohyala ignicolor* is nearly uniform green dorsally (pl. 67, fig. 3). The dorsum is pale green with irregular darker green markings and greenish yellow on the flanks. The anterior and posterior surfaces of the thighs, ventral surfaces of the shanks, anterior surfaces of the tarsi, and upper proximal surfaces of the first, second, and third toes are red or orange-red. A narrow creamy tan line is present on the outer edges of the tarsi, and a faint creamy white line is present above the anus. The venter is pale creamy yellow, and the ventrolateral glands are pale orange-tan. The iris is pale gold.

In preservative the dorsum is pale brown with dark brown reticulations on the head and body and dark brown transverse bands or spots on the limbs. The first and second fingers are cream, and the third is brown. The dorsal surfaces of the tarsi and the third, fourth, and fifth toes are dull brown with dark brown spots. The first and second toes are creamy white. The webbing on the foot is brown. The axilla and groin are creamy white. The flanks are brown. The throat, belly, and ventral surfaces of the limbs are creamy white; the chest and throat are spotted with brown. The ventrolateral and chin glands are orange-brown.

All specimens were pale green above when found at night; later most changed to dull

green with darker green reticulations. The flash color on the thighs and in the groin vary from red to orange-red or orange-brown. The white anal stripe varies from a thin line to a series of white flecks. Dark brown or black flecks are present on the throat, chest, and flanks of all specimens. In some the flecks are small and widely scattered; in others the flecks are larger and more numerous.

**TADPOLES:** A typical tadpole in developmental stage 28 has a total length of 38 mm. and a body length of 12.1 mm. The body is moderately depressed and only slightly wider than deep; in dorsal profile the body is ovoid and widest just posterior to the eyes. In lateral profile the snout is rounded. The mouth is directed ventrally. The eyes are small and directed dorsolaterally; the nostrils are barely protuberant, directed anteriorly and situated about midway between the eyes and the tip of the snout. The spiracle is sinistral and posteroventral to the eye; the anal tube is dextral. The tail is long and slender. The caudal fins are low and rounded posteriorly. The caudal musculature is robust and does not reach the tip of the tail. The dorsal fin barely extends onto the body and is deepest at about midlength of the tail; the ventral fin has an equal depth throughout most of its length (fig. 260B).

The mouth is large; the thin fleshy lips are greatly expanded and form a large funnel-shaped disc. The width of the mouth is about two-thirds the greatest width of the body. The lips are completely bordered by a row of small papillae. The inner surface of the mouth is smooth except for scattered large papillae. One large papilla is present just above the lateral edge of the first lower tooth row. The beaks are robust; the upper beak forms a broad arch and lacks lateral processes. Both beaks bear long pointed serrations. There are three upper and three lower rows of teeth. All rows are short; the second and third upper rows are about equal in length, whereas the first upper row is noticeably shorter. The first lower row is as long as the third upper row, whereas the second and third lower rows are progressively shorter. The first and third upper rows and the first lower row are narrowly interrupted medially (fig. 261E).

The body is creamy gray with dark brown flecks above and below; the mouth is colored like the body. The caudal musculature is creamy tan, and the caudal fin is transparent. A dark brown streak is present on the anterior one-third of the caudal musculature; the rest of the tail and all of the caudal fin except the anterior two-thirds of the ventral fin, are heavily flecked with brown. The iris is pale, silvery bronze.

**MATING CALL:** The call of *Ptychohyla ignicolor* consists of a series of short notes, three to 13 notes per series. The notes are raucous and low-pitched. The duration of each note is about 0.08 seconds. There are 123 to 129 pulses per second. The dominant frequency is at about 2100 cycles per second in short series of notes and at about 3150 cycles per second in long series of notes (pl. 30, fig. 2).

**NATURAL HISTORY:** *Ptychohyla ignicolor* inhabits cascading mountain streams in cloud forests. Calling males have been found from February through August, and probably breeding takes place throughout most, if not all, of the year. Males call from bushes and low trees at the edge of, and overhanging, the streams.

Tadpoles have been found in shallow, gravel-bottomed pools in the streams. There the tadpoles cling to the pebbles on the bottom and take refuge amidst leaf litter and other stream-bottom detritus.

**REMARKS:** *Ptychohyla ignicolor* is a distinctive species and apparently represents the only member of the *Ptychohyla schmidtorum* group west of the Isthmus of Tehuantepec. In the vicinity of Campamento Vista Hermosa, in northern Oaxaca, the species occurs in the same streams with *Ptychohyla leonhardschultzei*.

**ETYMOLOGY:** The specific name *ignicolor* is Latin and means "flame-colored"; the name alludes to the flash-color on the thighs.

**DISTRIBUTION:** *Ptychohyla ignicolor* inhabits the cloud forests on the northern slopes of the Sierra de Juárez in northern Oaxaca, México, where it has been taken at elevations between 1500 and 1850 meters (fig. 263).

See Appendix 1 for the locality records of the 69 specimens examined.

*Ptychohyla euthysanota* (Kellogg)

*Hyla euthysanota* Kellogg, 1928, p. 123 [holotype, U.S.N.M. No. 73296 from Los Esemiles, Departamento Chalatenango, El Salvador; Ruben A. Stirton collector].

**DIAGNOSIS:** This species is distinguished from other *Ptychohyla* by having a tarsal fold, a moderate amount of webbing on the hand, and small spinous nuptial excreseences on the thumb in breeding males. *Ptychohyla euthysanota* can be distinguished from *spinipollex* and *leonhardschultzei* by lacking a vertical rostral keel and large spots in the groin, and by having smaller nuptial spines.

**CONTENTS:** Two subspecies are recognized: *Ptychohyla euthysanota euthysanota* (Kellogg) inhabits the Pacific versant of the Sierra Madre from extreme eastern Oaxaca, México, to El Salvador and *P. euthysanota macrotympa-num* (Tanner) occurs in the Central Highlands of Chiapas and in the Grijalva Valley of Chiapas and Guatemala.

*Ptychohyla e. euthysanota* has slightly shorter limbs and smaller feet and head than *macrotympa-num*. The subspecies are most easily distinguished by differences in color.

The nominate subspecies has a darker dorsum, broader stripe on upper lip, and a distinct lateral stripe.

**DISTRIBUTION:** *Ptychohyla euthysanota* occurs at elevations of 660 to 2200 meters in the Central Highlands of Chiapas, in the Grijalva Valley in Chiapas and Guatemala, and in the Sierra Madre from Oaxaca to El Salvador (fig. 264).

*Ptychohyla euthysanota euthysanota* (Kellogg)

*Hyla euthysanota* Kellogg, 1928, p. 123 [holotype, U.S.N.M. No. 73296 from Los Esemiles, Departamento Chalatenango, El Salvador; Ruben A. Stirton collector].

*Hyla rozellae* Taylor, 1942c, p. 78 [holotype, U.S.N.M. No. 115039 from Salto de Agua, Chiapas, México; Hobart M. and Rozella Smith collectors]. Smith and Taylor, 1948, p. 86.

*Ptychohyla bogerti* Taylor, 1949b, p. 13 [holotype, A.M.N.H. No. 51847 from Río Grande, Oaxaca, México; Thomas MacDougall collector].

*Ptychohyla euthysanota*: Duellman, 1961b, p. 351 [transfer of *Hyla euthysanota* Kellogg, 1928 to the genus *Ptychohyla* Taylor, 1944a]. Stuart, 1963, p. 40.

*Ptychohyla rozellae*: Gorham, 1963, p. 24.

*Ptychohyla euthysanota euthysanota*: Duellman, 1963c, p. 315 [synonymized *Hyla rozellae* Taylor,

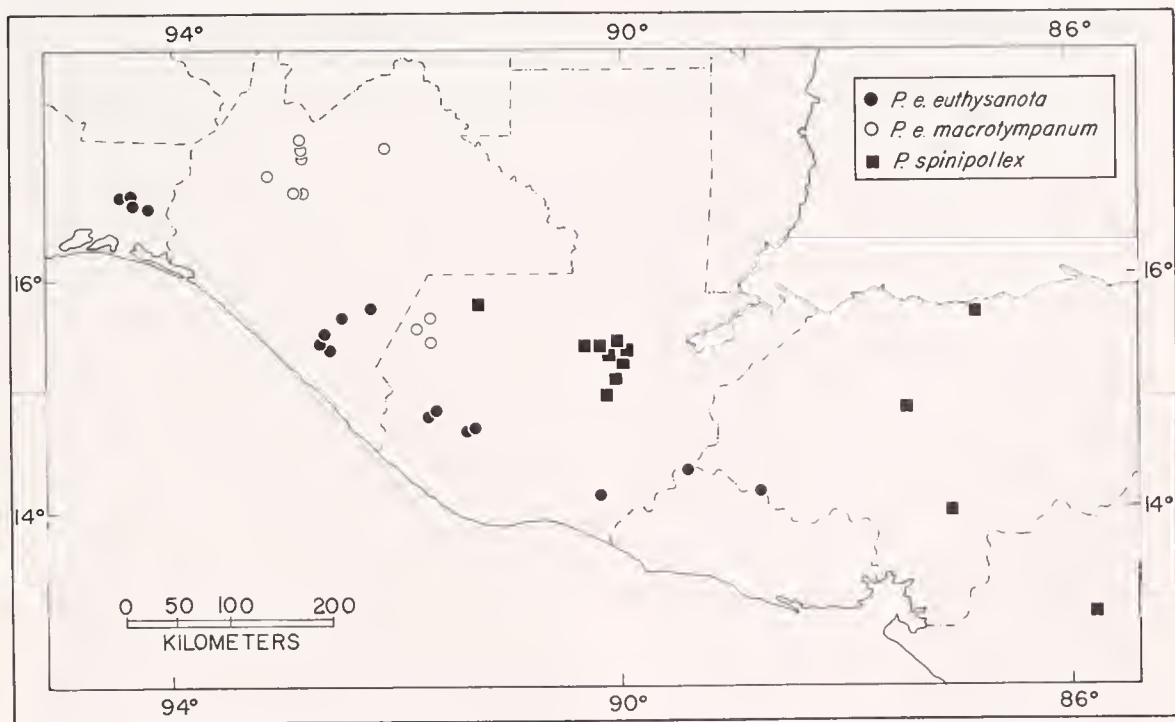


FIG. 264. Distribution of *Ptychohyla spinipollex* and the subspecies of *Ptychohyla euthysanota*.



1942c, and *Ptychohyla bogerti* Taylor, 1949b, with *Ptychohyla euthysanota euthysanota* (Kellogg, 1928)].

**DIAGNOSIS:** This subspecies is distinguished from *P. euthysanota macrotympanum* by having a reddish tan or brown dorsum and a white venter that rarely is marked with brown or black flecks, whereas *macrotympanum* has a pale tan dorsum and heavily flecked venter. A distinct lateral white stripe is present in the nominate subspecies, whereas the stripe is either lacking or indistinct in *macrotympanum*.

**DESCRIPTION:** Males of this moderate-sized frog attain a maximum snout-vent length of 38.1 mm. (mean, 17 specimens from Finca La Paz, Departamento San Marcos, Guatemala, 35.0 mm.), and females reach 43.3 mm. (mean, 15 specimens, 38.2 mm.). In the sample of 17 males from Finca La Paz, the ratio of tibia length to snout-vent length is 0.444 to 0.550 (mean, 0.487); the ratio of foot length to snout-vent length is 0.349 to 0.405 (mean, 0.380); the ratio of head length to snout-vent length is 0.293 to 0.318 (mean, 0.307); the ratio of head width to snout-vent length is 0.296 to 0.312 (mean, 0.304), and the ratio of the tympanum to that of the eye is 0.486 to 0.638 (mean, 0.563).

The head is about as wide as the body; the top of the head is slightly convex. The interorbital distance is noticeably wider than the eyelid; the ratio of the width of the eyelid to that of the inner orbital space is 0.679 to 0.732 (mean, 0.714). In dorsal profile the snout is bluntly pointed; in lateral profile the snout is rounded. The snout is moderately long; the nostrils are barely protuberant and are situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is slightly elevated and angular; the loreal region is concave and the lips are moderately thick and barely flared. A heavy dermal fold extends posteriorly from the eye above the tympanum to a point above the insertion of the arm; the fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arm is short and robust; an abbreviated axillary membrane is present. A row of

small tubercles forms an indistinct ridge on the ventrolateral surface of the forearm; a distinct transverse fold is present on the wrist. The fingers are moderate in length and rather robust. The terminal discs are moderately large; that on the third finger is slightly larger than the diameter of the tympanum. The subarticular tubercles are large and subconical; the distal tubercle on the fourth finger is bifid in about two-thirds of the specimens. Moderate-sized, round, supernumerary tubercles are present on the proximal segments of the second, third, and fourth fingers. No distinct palmar tubercles are present although a cluster of small tubercles is present on the palm. The prepollex is moderately large; in breeding males the nuptial excrecence consists of a cluster of small spines; on each thumb there is 44 to 143 (mean, 83.8) spines. The fingers are about one-third webbed (fig. 257B). The web is vestigial between the first and second fingers, but extends from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels barely overlap. The tibiotarsal articulation extends to the eye. A low, rounded tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, elliptical, and barely visible from above. The outer metatarsal tubercle is small, round, and indistinct. The toes are long and slender. The terminal discs are only slightly smaller than those on the fingers. The subarticular tubercles are large and round; low, indistinct supernumerary tubercles are present on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 258B). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third and from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. The opening is bordered on either side by heavy dermal folds and covered by a thin, short anal flap. The skin on the dorsum and ventral surfaces of the limbs is smooth; that on the throat, belly, and posteroventral surfaces of the thighs is granular. The ventrolateral glands are moderately developed; they do not reach the axilla nor the groin and are broadly separated midventrally. The tongue is ovoid, usually marginate, and only slightly free posteriorly. In about 20 per cent of the specimens the tongue is shallowly notched posteriorly. Males have four to six (mean, 5.1) prevomerine teeth and females have six to 18 (mean, 9.6) prevomerine teeth situated on small triangular elevations between small ovoid choanae. The vocal slits extend from the midlateral base of the tongue to the angle of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Ptychohyla euthysanota euthysanota* is reddish brown with small indistinct darker brown markings on the dorsum and a distinct white stripe on the flanks (pl. 67, fig. 4). The dorsal ground color usually is pale reddish brown; the dorsal reticulations are dark brown. Indistinct, usually incomplete, brown transverse bands are present on the limbs. The posterior surfaces of the thighs are pale reddish brown. The dorsal surfaces of the first and second fingers and the webbing on the hands are creamy tan; the webbing on the feet is gray. A faint creamy white stripe is present along the lateral edges of the tarsi and forearm; a thin white line is present along the edge of the upper lip and a distinct white stripe is present above and beside the anal opening. The axilla is white; the throat, chest, belly and ventral surfaces of the limbs are creamy white. The ventral coloration is separated from the white stripe on the flank by a row of small dark brown spots. The ventrolateral glands are cream colored. The iris is reddish bronze.

In preservative the dorsal ground color is dull reddish brown with irregular dark brown markings. The white markings on the limbs, flanks, and above the anus persist in the preserved specimens. The ventral surfaces of the

thighs are dull creamy yellow and the feet are grayish brown. The ventrolateral glands are pale grayish brown.

Most individuals when collected at night had a pale reddish brown dorsum; one individual had dull olive-green reticulations on the back and transverse bands on the limbs; the dorsal surfaces of the first and second fingers and the discs on the third and fourth fingers were orange. The distinctness of the white stripe on the upper lip is variable; in two individuals the stripe is barely discernible. Likewise, in some individuals the white stripe on the flank is not distinct, either because there are few or no brown spots separating the stripe from the pale venter, or because the ventrolateral gland has diffused the pale color on the flanks. There is some noticeable variation in dorsal coloration, either in the greater or lesser development of dark pigment. One specimen (K.U. No. 58007) is grayish tan above with dark brown markings; the posterior surfaces of the thighs are dull grayish yellow, and the first and second fingers and the webbing on the hands are pale yellowish gray. The belly and throat are dusky white, and gray flecks are present on the throat. Dark individuals, such as one from Finca La Paz (K.U. No. 58009), have a uniform dark brownish black dorsum; the belly is cream, and the first and second fingers and the webbing on the hands is dull creamy tan. The dorsal and ventral surfaces of the feet are dark brown. One individual from Finca La Paz (K.U. No. 58013) has a heavy suffusion of brown on the throat and flanks. Two specimens have scattered white flecks on the dorsum.

The reddish brown dorsal ground-color with dark brown reticulations on the head and body and dark brown transverse bands on the limbs seems to be rather constant throughout the range of the subspecies. Likewise, the presence of the white stripe on the upper lip and the white stripe around the anal opening are present on most specimens. In breeding males having well-developed ventrolateral glands, the lateral white stripe is often obliterated.

**TADPOLES:** A series of tadpoles is available from Finca La Paz, Departamento San Marcos, Guatemala. A typical tadpole in de-

developmental stage 25 has a total length of 33.2 mm. and a body length of 11.6 mm. The body is moderately depressed and slightly wider than deep. In dorsal profile the body is ovoid; in lateral profile the snout is rounded. The mouth is directed ventrally. The eyes are small and directed dorsolaterally; the nostrils are slightly protuberant and are situated slightly closer to the tip of the snout than to the eyes. The spiracle is sinistral and posteroventral to the eyes; the anal tube is dextral. The tail is long and low. The caudal fins are shallow and pointed posteriorly. The caudal musculature is moderately heavy and extends nearly to the tip of the tail. The dorsal fin barely extends onto the body and is deepest at about two-thirds the length of the tail; the ventral fin has an equal depth throughout its length (fig. 260C).

The mouth is large and has well-developed lateral folds. The lips are completely bordered by two rows of small papillae; five or six rows of papillae are present in the lateral folds. The beaks are moderately robust and bear short peg-like serrations. The upper beak forms a broad arch and has short, slender, bluntly rounded lateral processes. There are four upper and six lower rows of teeth. All upper rows are approximately equal in length. The fourth upper row is always interrupted medially, and in many specimens the first upper row is interrupted medially. The first four lower rows are about equal in length and somewhat shorter than the upper rows, whereas the fifth and sixth lower rows are progressively shorter. The first lower row is usually interrupted medially. The fifth and sixth lower rows are sometimes fragmentary (fig. 261A).

The body is brown above and grayish cream below; the tip of the snout is cream. A cream tan crescent-shaped bar is present on the posterior edge of the body and the anterior part of the caudal musculature and is bordered posteriorly by a dark brown blotch. The caudal musculature creamy tan and marked with scattered brown flecks. The caudal fin is transparent; brown flecks are present on all of the dorsal fin and on the posterior half of the ventral fin. The cream, crescent-shaped mark usually is distinct. The brown blotch posterior to this mark is vari-

ously shaped, ranging from a narrow vertical bar to a triangular blotch. Brown flecks seldom are present on the anterior part of the ventral caudal fin.

**MATING CALL:** The call of *Ptychohyla euthysanota euthysanota* consists of a single soft note, "wraaaek." The notes were repeated at intervals of three or four seconds. Each note has a duration of 0.60 to 0.65 seconds and has 91 to 102 pulses per second; the dominant frequency is between 3000 and 3200 cycles per second.

**NATURAL HISTORY:** This subspecies lives in cloud forests and breeds in clear, swift mountain streams. Males call from stems and leaves of plants at the edge of, or overhanging, the streams. Tadpoles at various stages of development were found at Finca La Paz, Guatemala, in late July. It is possible that *Ptychohyla euthysanota euthysanota* breeds throughout the year, because of equitable climatic conditions and abundance of rainfall throughout the year in the cloud forest. This supposition is supported by the fact that tadpoles in stages 25 through metamorphosis were found in the same stream on the same day.

Two recently metamorphosed young have snout-vent lengths of 15.2 and 14.8 mm.; they are colored like the adults.

**REMARKS:** The type specimen of *Hyla euthysanota* Kellogg (1928) is a female; therefore, when Taylor (1944a) proposed the name *Ptychohyla* for hylids having ventrolateral glands in breeding males, he was unaware that *Hyla euthysanota* was a member of this group. In his description of *Hyla rozellae*, Taylor (1942e) did not compare his specimens with *Hyla euthysanota* but instead placed *rozellae* with *Hyla loquax* and *rickardsi* (= *godmani*). The type series of *Hyla rozellae* consists of one large adult female and several metamorphosing young. Taylor (1949b) based the description of *Ptychohyla bogerti* on two males and compared these specimens with *P. adipiventris* Taylor [= *P. leonhardschultzei* Ahl]. Thus, in a period of 22 years the females of this species were given two names and the males another. Stuart (1954b) suggested that *Hyla euthysanota* and *Hyla rozellae* were *Ptychohyla*. Duellman (1963e) placed *Hyla rozellae* Taylor and



*Ptychohyla bogerti* Taylor in the synonymy of *Ptychohyla euthysanota*. Furthermore, he demonstrated that *Hyla macrotympanum* Tanner was a subspecies of *Ptychohyla euthysanota*.

Lynch and Smith (1966) recorded a specimen of *Ptychohyla macrotympanum* from "Zanatepec, Oaxaca." I have examined this specimen (U.I.M.N.H. No. 56192), which actually was collected in the Sierra Madre north of Zanatepec. I am unable to distinguish this specimen from specimens of *Ptychohyla euthysanota* from the same area. I am convinced that Lynch and Smith were incorrect in their determination of the specimen and their assignment of *macrotympanum* to the specific status.

**ETYMOLOGY:** The trivial name *euthysanota* is derived from the Greek *eu-* meaning primitive and the Greek *thysanotos* meaning fringe; the name is in reference to the weak fringe-like row of tubercles on the edge of the forearm.

**DISTRIBUTION:** *Ptychohyla euthysanota euthysanota* inhabits cloud forests at elevations of 660 to 2200 meters on the Pacific slopes of the Sierra Madre from extreme Oaxaca and western Chiapas, México, through Guatemala to northern El Salvador (fig. 264).

In addition to the locality records of the 75 specimens examined, listed in Appendix 1, Mertens (1952b, p. 29) recorded the species from three localities in Departamento Santa Ana, El Salvador: Hacienda San José, Hacienda Los Planes, and Miramundo.

### *Ptychohyla euthysanota macrotympanum* (Tanner)

*Hyla macrotympanum* Tanner, 1957, p. 52 [holotype, A.M.N.H. No. 62141 (formerly B.Y.U. No. 13752) from 10 miles east of Chiapa de Corzo, Chiapas, México; Robert Bohlman collector].

*Ptychohyla macrotympanum*: Duellman, 1961b, p. 351 [transfer of *Hyla macrotympanum* Tanner, 1957, to the genus *Ptychohyla* Taylor, 1944a]. Stuart, 1963, p. 41. Lynch and Smith, 1966, p. 66.

*Ptychohyla euthysanota macrotympanum*: Duellman, 1963c, p. 320 [placed *Ptychohyla macrotympanum* (Tanner, 1957) as a subspecies of *Ptychohyla euthysanota* (Kellogg, 1928)].

**DIAGNOSIS:** This subspecies is distinguished from the nominate subspecies by hav-

ing a pale tan dorsum and dark flecks on the venter and by lacking a distinct lateral white stripe. *Ptychohyla e. euthysanota* has a reddish tan or brown dorsum, an immaculate venter, and a distinct white stripe on the flank.

**DESCRIPTION:** Males of this moderate-sized frog attain a maximum snout-vent length of 38.0 mm. (mean, 5 specimens from the Central Highlands of Chiapas, 34.9 mm.), and females reach 44.8 mm. (mean, 5 specimens, 39.7 mm.). In the sample of five males the ratio of the tibia length to snout-vent length is 0.488 to 0.520 (mean, 0.502); the ratio of foot length to snout-vent length is 0.405 to 0.424 (mean, 0.417); the ratio of head length to snout-vent length is 0.316 to 0.325 (mean, 0.319); the ratio of head width to snout-vent length is 0.313 to 0.319 (mean, 0.315), and the ratio of the diameter of the tympanum to that of the eye is 0.500 to 0.571 (mean, 0.541).

Structurally *Ptychohyla euthysanota macrotympanum* is like the nominate subspecies; the reader is referred to the account of *Ptychohyla euthysanota euthysanota* for a detailed description.

The general coloration of this subspecies is tan with dark brown flecks and reticulations (pl. 67, fig. 5). The dorsum is pale tan; in some specimens there is a pinkish tint on the flanks. The dorsum is marked with a dark reticulation or interconnecting flecks of dark brown. The dorsal surfaces of the limbs are marked by narrow, irregular dark brown bands. The posterior surfaces of the thighs are a dull tan. A thin, creamy white line is present on the outer edge of the forearm and the outer edge of the tarsus. A thin white line extends the length of the upper lip, and a grayish white line is present above the anus. There is no lateral white stripe. The belly is creamy white and the ventrolateral glands are slightly darker cream. A few dark flecks are present on the anterior half of the chin. The iris is dull coppery bronze.

In preservative the dorsum is pale pinkish tan with most of the head and body covered by large gray interconnecting blotches; black flecks occur over most of the dorsum. The posterior surfaces of the thighs are pale grayish yellow. The faint white lines on the

limbs, upper lip, and above the anus persist in preserved specimens. The venter is pale grayish white and the ventrolateral glands are pinkish tan.

Some specimens in life are brown with much darker brown markings on the dorsum. In these specimens, the posterior surfaces of the thighs are yellowish tan and heavily suffused with brown. Two individuals have small white flecks on the dorsum. The white line on the upper lip is present in all specimens, but in some individuals it is indistinct; the grayish white line above the anus is present in all specimens.

**TADPOLES:** A typical tadpole in developmental stage 25 from the Río Hondo, south of Pueblo Nuevo Solistahuacán, Chiapas, México, has a total length of 36.2 mm. and a body length of 11.1 mm. Structurally the tadpole is like that of the nominate subspecies. In tadpoles of *P. euthysanota macrotympenum* the body is brown above and creamy white below; the tip of the snout is cream. The caudal musculature is creamy tan and the caudal fin is transparent. There is a cream-colored, crescent-shaped mark on the posterior edge of the body and anterior part of the caudal musculature, bordered posterodorsally by a dark brown blotch. The caudal musculature is marked by dark brown blotches. There are scattered brown flecks on the posterior part of the musculature and on the caudal fin. The eye is silvery bronze in life. The dark blotches on the caudal musculature are most distinct in small specimens; in large individuals the tail is predominately marked by dark flecks.

**MATING CALL:** The call of *Ptychohyla euthysanota macrotympenum* is nearly identical to that of the nominate subspecies. The call consists of a soft note, "wraaack," repeated three to nine times with intervals of 2.7 to 3.4 seconds between the notes. Each note has a duration of 0.60 to 0.65 seconds, and 92 to 100 pulses per second; the dominant frequency is from 3000 to 3200 cycles per second (pl. 31, fig. 1).

**NATURAL HISTORY:** This subspecies lives in mixed pine and broad-leaved forest, where it breeds in clear mountain streams. The males call from trees and bushes along the streams. Tadpoles in various stages of de-

velopment were found in the Río Hondo, Chiapas, in June. A metamorphosing frog taken at the same time has a snout-vent length of 19.8 mm. and a short remnant of a tail. The mouth and tongue are developed, whereas another individual having a snout-vent length of 17.8 mm. and a tail 31.0 mm. in length still has larval teeth. Three completely metamorphosed juveniles collected by Dr. L. C. Stuart at Jacaltenango, Guatemala, on June 6 and 7 have snout-vent lengths of 16.0, 16.0, and 16.1 mm.

**REMARKS:** Tanner (1957) based the description of *Hyla macrotympenum* on a single female, which, of course, lacked the characters diagnostic of *Ptychohyla*. On the basis of general external characters, Tanner suggested that *Hyla macrotympenum* was related to *H. miotympanum* from which it differs in having a larger tympanum and bifid subarticular tubercle beneath the fourth finger. Duellman (1963c) showed that *macrotympenum* was actually a *Ptychohyla* and subspecifically related to *P. euthysanota*.

The specimen reported as *Ptychohyla macrotympenum* by Lynch and Smith (1966) from Zanatepee, Oaxaca, actually is a specimen of *Ptychohyla euthysanota euthysanota*. There is no evidence that *macrotympenum* is specifically distinct from *euthysanota*. In fact, the subspecies are rather weakly differentiated.

**ETYMOLOGY:** The trivial name *macrotympenum* is derived from the Greek *makros* meaning long, and the Greek *tympanon* meaning drum. Tanner used the name in reference to the large tympanum in comparison with that of *Hyla miotympanum*, which he thought to be closely related to his new species; furthermore, Tanner used the Greek *makros* to mean large, when correctly the word means long.

**DISTRIBUTION:** *Ptychohyla euthysanota macrotympenum* occurs in mixed pine and broad-leaved forests at elevations of 700 to 1700 meters on the southern slopes of the Chiapan Highlands and Sierra de los Cuchumatanes, Guatemala, and in the upper part of the Grijalva Basin in Chiapas, in Guatemala and Chiapas, México (fig. 264).

See Appendix 1 for the locality records of the 23 specimens examined.

***Ptychohyala leonhardschultzei* (Ahl)**

*Hyla leonard-schultzei* Ahl, 1934, p. 185 [holotype, Z.M.B. No. 34353 from Malinaltepec, Guerrero, México; Leonhard Schultz collector]. Smith and Taylor, 1948, p. 87.

*Hyla godmani*: Ahl, 1934, p. 186 [erroneous identification].

*Ptychohyala adipoventris* Taylor, 1944a, p. 41 [holotype, U.I.M.N.H. No. 25047 (formerly E.H.T.-H.M.S. No. 21592) from Agua del Obispo, Guerrero, México; Edward H. Taylor, collector]. Smith and Taylor, 1948, p. 91.

*Hyla milleri* Shannon, 1951, p. 473 [holotype, U.S.N.M. No. 123700 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector].

*Ptychohyala leonhard-schultzei*: Duellman, 1960c, p. 191 [synonymized *Ptychohyala adipoventris* Taylor, 1944a, and *Hyla milleri* Shannon, 1951, with *Ptychohyala leonhard-schultzei* (Ahl, 1934); erroneously synonymized *Hyla pinorum* Taylor, 1937, with *Ptychohyala leonhard-schultzei* (Ahl, 1934)].

*Ptychohyala leonhardschultzei*: Duellman, 1963c, p. 323.

**DIAGNOSIS:** This moderate-sized species has a tarsal fold, rostral keel, and fingers about one-third webbed. The nuptial spines are moderately small, and the interorbital distance is much greater than the width of the eyelid. *Ptychohyala spinipollex* resembles *leonhardschultzei* but differs in having a snout that is rounded above, instead of angularly truncate, and in having a narrower interorbital space and larger nuptial spines.

**DESCRIPTION:** Males of this moderate-sized species attain a maximum snout-vent length of 35.6 mm. (mean, 20 specimens from the mountains north of San Gabriel Mixtepec, Oaxaca, México, 31.6 mm.), and females reach 43.4 mm. (mean, 8 specimens, 39.9 mm.). In this sample of 20 males the ratio of tibia length to snout-vent length is 0.472 to 0.544 (mean, 0.512); the ratio of foot length to snout-vent length is 0.386 to 0.455 (mean, 0.426); the ratio of head length to snout-vent length is 0.311 to 0.345 (mean, 0.326); the ratio of head width to snout-vent length is 0.324 to 0.351 (mean, 0.340), and the ratio of the diameter of the tympanum to that of the eye is 0.477 to 0.559 (mean, 0.511). Comparison of samples from the Pacific slopes of Guerrero, from the Pacific slopes of Oaxaca, and from the Atlantic slopes of Oaxaca reveal that there are no significant differences in size or proportions. Females have slightly

larger tympani than do males; in the sample from the mountains north of San Gabriel Mixtepec, the ratio of the diameter of the tympanum to that of the eye is 0.486 to 0.619 (mean, 0.563) in eight females.

The head is as wide as the body; the top of the head is slightly convex. The inner orbital distance is much greater than the width of the eyelid; the ratio of the width of the eyelid to that of the interorbital space is 0.639 to 0.681 (mean, 0.652). In dorsal profile the snout is rounded with a terminal point, resulting from the fleshy, vertical rostral keel. In lateral profile the snout is truncate. The snout is moderately long; the nostrils are noticeably protuberant and are situated at about four-fifths the distance from the eyes to the tip of the snout. The canthus is angular; the loreal region is barely concave, and the lips are thick and only moderately flared. A heavy dermal fold extends posteriorly from the posterior corner of the eye above the tympanum and curves downward to a point above the insertion of the arm. The fold covers the upper edge of the tympanum, which otherwise is distinct. The tympanum is situated posteroventrally to the eye and is separated from the eye by a distance about equal to the diameter of the tympanum.

The arm is moderately short, but slender. An abbreviated axillary membrane is present. A row of tubercles along the ventrolateral edge of the forearm forms an indistinct fold; a thin transverse dermal fold is present on the wrist. The fingers are relatively short and broad, and bear moderate discs; the disc on the third finger is about the size of the tympanum. The subarticular tubercles are moderately large and round; the distal tubercle on the fourth finger is divided or bifid in most specimens, and the distal tubercle on the third finger is bifid in some specimens. Small, indistinct supernumerary tubercles are present on the proximal segments of the second, third, and fourth fingers. A low, flat, triangular palmar tubercle is present; usually it is bordered medially by two smaller, higher tubercles. The prepollex is moderately enlarged; in breeding males the nuptial excrescence consists of 24 to 80 (mean, 54.7) spines. The hands are about one-third webbed (fig. 257D). The webbing



is vestigial between the first and second fingers, but extends from the basal part of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third and from the base of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A low, rounded tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, ovoid, and barely visible from above. A minute, usually indistinct, outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately small, round, and subconical. Small, indistinct, supernumerary are present on the proximal segments of each toe. The toes are about three-fourths webbed (fig. 258D). The web extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the level of the upper edges of the thighs. The anal sheath is short. The anal opening is bordered laterally by heavy dermal folds and ventrolaterally by large tubercles. The skin on the dorsum and ventral surfaces of the forelimbs and shanks is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. The ventrolateral glands are moderately developed; they reach the axilla, but not quite to the groin and are broadly separated midventrally. The tongue is cordiform, shallowly notched behind, and barely free posteriorly. Males have six to nine (mean, 6.5) prevomerine teeth, and females have seven to 12 (mean, 9.5) prevomerine teeth situated on transverse elevations between the ovoid choanae. The vocal slits extend from the midlateral base of the tongue

to the angles of jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Ptychohyla leonhardschultzei* is dull brown or reddish brown with faintly darker brown markings on the dorsum (pl. 67, fig. 6). The dorsum varies from tan to brown or reddish brown with large interconnected dark brown blotches on the head and body and broad dark transverse bands on the limbs. The dorsal surfaces of the first and second fingers and the webbing on the hands is pale brown or reddish brown. The webbing on the feet is dark brown. The flanks are pale creamy white with dark brown or black spots. In some individuals the groin has a distinct yellow tint. The posterior surfaces of the thighs are dull tan, and the anterior surfaces are pinkish tan or lack pigment entirely. Narrow white stripes are present on the ventrolateral edges of the forearms and tarsi, and a faint creamy white stripe extends above the anal opening. The throat and belly are white; large brown spots are present on the chin and anterior part of the abdomen. The ventrolateral glands are creamy tan. The iris is reddish bronze.

In preservative the dorsal surfaces are pale tan to dull brown, and the dorsal markings are dark brown. The posterior surfaces of the thighs are brown, and the flanks are creamy white.

Some individuals are pale yellowish tan when active at night; these individuals are usually less boldly marked than are those having darker pigmentation. In most individuals the white color in the axilla extends on to the posterior edge of the upper arm. The creamy white color of the flanks is constant and usually extends slightly dorsad in the inguinal region. The white stripe above, and sometimes continuing down beside, the anal opening varies from a thin indistinct line or row of flecks to a distinct continuous stripe. In most specimens ventral spots are confined to the throat and anterior part of the abdomen, but a few specimens have dark brown spots over the entire belly.

Specimens from the Pacific slope of Oaxaca tend to have a distinct narrow white labial stripe that is expanded to form a white suborbital spot. The upper lip and suborbital

region in specimens from northern Oaxaca often is a paler color than the rest of the head, but no distinct stripe or spot is present. One specimen when found at night was dull brown with orange blotches on the dorsum, and another was pale tan with dull olive-green markings on the dorsum. Specimens from the southern part of Oaxaca tend to have more brightly colored thighs than do those from the Atlantic slopes of Oaxaca; specimens from the mountains north of San Gabriel Mixtepec have orange-tan or orange-brown color on the anterior and posterior surfaces of the thighs. Furthermore, in these specimens, the flanks tend to be silvery white with distinct bold black spots.

**TADPOLES:** A typical tadpole in developmental stage 26 has a total length of 38.5 mm. and a body length of 12.1 mm. The body is slightly depressed and barely wider than deep; in dorsal profile the body is ovoid. In lateral profile the snout is bluntly rounded. The mouth is ventral. The eyes are small and are directed dorsolaterally; the nostrils are barely protuberant and directed anterolaterally and are situated about midway between the eyes and the tip of the snout. The spiracle is sinistral and posteroventral to the eyes; the anal tube is dextral. The tail is long, low, and pointed. The caudal musculature is moderately robust and terminates just short of the tip of the tail. The dorsal fin barely extends onto the body and reaches its greatest depth at about mid-length of the tail, whereas the ventral fin maintains an equal depth throughout most of the length of the tail (fig. 260D).

The mouth is large; the lips have deep lateral folds. Two rows of small papillae completely border the lips; five to seven rows of papillae are present in the lateral fold. The beaks are moderately robust and bear short, peg-like serrations. The upper beak forms a broad arch with slightly curved, slender, blunt lateral processes. There are four upper and six lower rows of teeth. The first three upper rows are complete and about equal in length, whereas the fourth upper row is shorter and interrupted medially. The lower rows are about equal in length, but shorter than the upper rows; the first lower row is interrupted medially. The teeth on

the fifth and six lower rows are less well developed than those in the other rows; in a few specimens a fragmentary seventh lower tooth row is present (fig. 261B).

The body is brown above and creamy gray below. The tip of the snout is brown. The caudal musculature is creamy tan and the caudal fin is transparent. A creamy white, crescent-shaped mark is present on the posterior edge of the body. The caudal musculature is marked by large dark brown square blotches on the dorsal surface or by irregular brown reticulations; small brown flecks are present on the caudal fins except on the anterior half of the ventral fin which is unmarked. The eye is reddish bronze in life.

**MATING CALL:** The call of *Ptychohyala leonhardschultzei* consists of a single note, "wraaek," repeated at intervals from several seconds to three or four minutes. Each note has a duration of 0.62 to 0.95 seconds and 76 to 78 pulses per second; the dominant frequency varies from 2700 to 2800 cycles per second (pl. 31, fig. 2).

**NATURAL HISTORY:** *Ptychohyala leonhardschultzei* inhabits cloud forests that have equable climatic conditions throughout the year. Field observations of this species on the northern slopes of the Sierra de Juárez in northern Oaxaca and in the mountains north of San Gabriel Mixtepec in southern Oaxaca, indicate that the species probably is active throughout the year. Breeding takes place in small streams, and males call from low bushes and trees at the edge of, or overhanging the streams.

The tadpoles live in the mountain streams, where they inhabit ripples or pools. At a small stream south of Yetla, in northern Oaxaca, tadpoles were taken from a quiet pool at the base of a small waterfall. The majority of the tadpoles were adhering to undersides of logs and branches in the pool. Others were lying on the mud at the bottom of the pool. When they were disturbed the tadpoles buried themselves in the mud.

Two recently metamorphosed young have snout-vent lengths of 15.2 and 15.5 mm.

**REMARKS:** Duellman (1960c) discussed the synonymy of *Ptychohyala leonhardschultzei*. He demonstrated that the frog named *Ptychohyala adipoventris* by Taylor

(1944a) had actually been described ten years earlier as *Hyla leonhard-schultzei* by Ahl (1934). Furthermore, Duellman placed *Hyla milleri* Shannon (1951) from San Lucas Camotlán, Oaxaca, in the synonymy of *Ptychohyla leonhardschultzei*. No evidence has come to light to change these conclusions. However, Duellman also placed *Hyla pinorum* Taylor (1937) in the synonymy of *Ptychohyla leonhardschultzei*. His action was based solely upon the examination of the type specimen (U.I.M.N.H. No. 25049) of *pinorum* from Agua del Obispo, Guerrero. This specimen is a small female and has no distinctive coloration. Independent field work in Guerrero in the summer of 1964 by the author and by Dr. Kraig Adler resulted in the acquisition of additional specimens of *Hyla pinorum*, a species now recognized as distinct from *Ptychohyla leonhardschultzei*. Consequently, Duellman (1960c) was in error in placing *Hyla pinorum* in the synonymy of *Ptychohyla leonhardschultzei*.

**ETYMOLOGY:** The specific name is a patronym for Leonhard Schultze, who obtained the type specimen.

**DISTRIBUTION:** *Ptychohyla leonhardschultzei* is known from pine-oak forest and cloud forest on the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca and from the Atlantic slopes of the Sierra de Juárez in northern Oaxaca, México (fig. 265).

Specimens have been collected at elevations between 700 and 2000 meters.

See Appendix 1 for the locality records of the 111 specimens examined.

### *Ptychohyla spinipollex* Schmidt

*Hyla cuthysanota*: Dunn and Emlen, 1932, p. 25 [erroneous identification].

*Hyla spinipollex* Schmidt, 1936, p. 45 [holotype, M.C.Z. No. 21300 from "mountains behind Ceiba," Departamento Atlántida, Honduras; Raymond E. Stadelman collector].

*Ptychohyla spinipollex*: Stuart, 1954b, p. 48; 1963, p. 41. Duellman, 1963c, p. 327.

**DIAGNOSIS:** This medium-sized species has a tarsal fold, rostral keel, and fingers about one-third webbed. The nuptial spines are moderately large, pointed, and few in number. The eyelid is about as wide as the interorbital space, and the snout is rounded above. *Ptychohyla spinipollex* differs from *leonhardschultzei* by having fewer and larger nuptial spines, relatively narrower interorbital space, and rounded, instead of an angular snout.

**DESCRIPTION:** This is the largest species in the genus of *Ptychohyla*. Males attain a maximum snout-vent length of 41.2 mm. (mean, 32 specimens from Finca Los Alpes, Alta Verapaz, Guatemala, 37.1 mm.), and females reach 44.6 mm. (mean, 6 specimens, 42.8 mm.). In the sample of males from

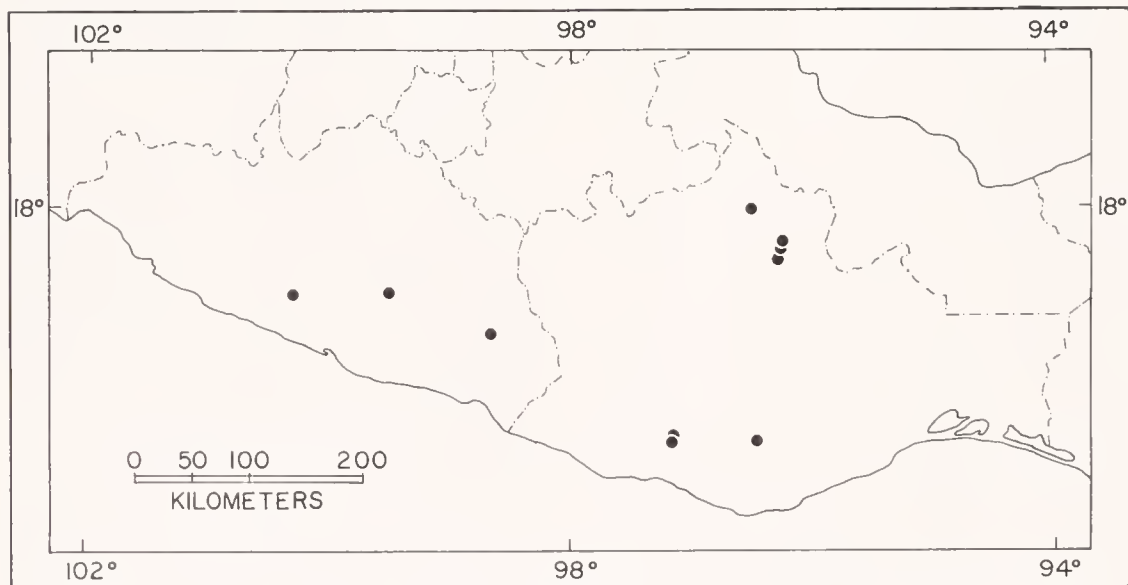


FIG. 265. Distribution of *Ptychohyla leonhardschultzei*.



Finca Los Alpes, the ratio of tibia length to snout-vent length is 0.469 to 0.531 (mean, 0.490); the ratio of the foot length to snout-vent length is 0.388 to 0.426 (mean, 0.408); the ratio of head length to snout-vent length is 0.308 to 0.335 (mean, 0.321); the ratio of head width to snout-vent length is 0.296 to 0.322 (mean, 0.311), and the ratio of the diameter of the tympanum to that of the eye is 0.450 to 0.552 (mean, 0.495). An insufficient number of well-preserved specimens are available from other parts of the range in order to determine if there is any geographic variation in size and proportions.

The head is as wide as the body; the top of the head is flat. The interorbital distance is only slightly greater than the width of the eyelid; the ratio of the width of the eyelid to that of the interorbital space is 0.878 to 0.923 (mean, 0.905). In dorsal profile the snout is bluntly rounded with a terminal point resulting from the presence of a vertical, fleshy rostral keel. In lateral profile the snout is rounded above and truncate. The snout is moderately long; the nostrils are situated at a point about three-fourths the distance from the eye to the tip of the snout. The canthus is angular; the loreal region is barely concave, and the lips are thick and moderately flared. A moderately heavy dermal fold extends posteriorly from the posterior corner of the eye above the tympanum to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posteroventral to the eye and separated from the eye by a distance equal to the diameter of the tympanum.

The arm is moderately short and robust. A short axillary membrane is present. A row of low tubercles forms a distinct ridge on the ventrolateral edge of the forearm; a weak transverse fold is present on the wrist. The fingers are moderately short and stout and bear relatively large discs; the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and round; in about two-thirds of the specimens the distal tubercle on the fourth finger is bifid. Small, subconical supernumerary tubercles are present on the proximal segment of each digit. A low bifid palmar tubercle is present. The prepollex is moder-

ately enlarged; in breeding males the nuptial excrecence is in the form of 35 to 66 (mean, 47.4) sharply pointed spines. The fingers are about one-third webbed (fig. 257E). The web between the first and second fingers is vestigial, but connects the second finger at the middle of the penultimate phalanx to the middle of the antepenultimate phalanx of the third and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are relatively short and robust; the adpressed heels barely overlap. The tibiotarsal articulation extends to the middle of the eye. A distinct, but low and rounded, tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, ovoid or quadrangular, and visible from above. The outer metatarsal tubercle is low, round, and distinct in most specimens. The toes are long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and subconical. Numerous small, round supernumerary tubercles are present on the proximal segments of each toe. The toes are about three-fourths webbed (fig. 258E). The web extends from the base of the disc of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the third, and from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and onto the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs; the opening is bordered laterally by moderately heavy dermal folds and ventrolaterally by tubercles. The anal sheath is short and thin. The skin on the dorsum and the ventral surfaces of the forelimbs and shank is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. The ventrolateral glands extend from the axilla for about two-thirds the length of the body; they do not reach the groin and are broadly separated midventrally. The tongue is ovoid, marginate or shallowly notched posteriorly, and barely free behind. Males have three to seven (mean, 4.9) prevomerine teeth, and females have six to 10 (mean, 7.6) prevomerine teeth situ-

ated on transverse or posteromedially slanting ridges between the ovoid choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Ptychohyla spinipollex* is yellowish tan with small irregular brown markings on the dorsum (pl. 67, fig. 7). A typical specimen from northern Guatemala has a yellowish tan dorsum with brown and dark brown markings on the back. In most individuals, the markings consist of small interconnected spots and dark brown flecks. Irregularly shaped dark marks on the limbs tend to form transverse bands. The posterior surfaces of the thighs are creamy tan. The first and second fingers are creamy tan, and the third and fourth fingers and webbing on the hand are grayish brown. The webbing on the feet is dark brown. The axilla is pale pink, and the flanks are buff, becoming yellow in the groin. The flanks are marked by dark brown spots. There is a faint white stripe along the ventrolateral edges of the forearms and tarsi, and a narrow white line above and beside the anal opening. There is no white stripe on the edge of the upper lip. The belly is dusky cream with numerous brown to dark gray flecks. The ventrolateral glands are grayish tan. The iris is dull grayish bronze.

A typical specimen from Honduras (K.U. No. 103225, from Cerro Uyuea) had in life a tan dorsum with olive-gray markings. The flanks were white with dark brown spots. The groin, anterior and posterior surfaces of the thighs were dull yellow, and the belly was immaculate white. The iris was dull grayish bronze.

In preservative the dorsum varies from grayish tan to dark brown with darker brown or black reticulations on the head and body and dark brown transverse bars or spots on the limbs. The anterior surfaces of the thighs are reddish tan, and the posterior surfaces are yellowish tan. The white stripes characteristic of living individuals persist in preserved specimens. The belly is dull white with scattered brown flecks; the flanks are grayish white with dark brown spots. The ventrolateral glands are grayish tan.

In specimens from Finca Los Alpes, Gua-

temala, the color of the dorsum varies from pale tan to dark brown with darker brown markings; the white line above the anus is present in all specimens, but it is indistinct in some. Two individuals have a dark brown dorsum with large pale tan square blotches; in life the blotches were pale tan and the dorsum was dark brown. All Guatemalan specimens have dark brown spots and flecks on the venter. Some individuals have only a few flecks on the throat and a few large spots on the flanks. Other specimens have dense spotting over the entire venter. One individual was dark brown with many small white flecks on the dorsum. All Honduran specimens either have an unmarked white venter or only a few small flecks on the edge of the chin. Furthermore, the Honduran specimens have fewer and smaller dark spots on the flanks, which tend to be paler than the flanks in Guatemalan specimens.

**TADPOLES:** A typical tadpole in developmental stage 31 from Finca Los Alpes, Alta Verapaz, Guatemala, has a total length of 38.7 mm. and a body length of 14.0 mm. The body is rounded and not depressed; it is as wide as deep and ovoid in dorsal profile. The mouth is directed ventrally. The eyes are small and directed dorsolaterally. The nostrils are barely protuberant and are directed anterolaterally; the nostrils are slightly closer to the tip of the snout than to the eyes. The spiracle is sinistral and posteroventral to the eye; the anal tube is dextral. The tail is long, low, and pointed posteriorly. The caudal musculature is heavy and nearly extends to the tip of the tail. The dorsal fin barely extends onto the body and reaches its greatest depth at the mid-length of the tail; the ventral fin has an equal depth throughout most of its length (fig. 260E).

The mouth is large and has deep lateral folds in the lips, which are bordered by two rows of small papillae; four or five additional rows of papillae are present in the lateral fold. The beaks are robust and bear short, peg-like serrations. The upper beak forms a broad arch with short, slender, round lateral processes. There are four upper and six or seven lower rows of teeth. The upper rows are about equal in length, and the fourth row is interrupted medially. The first four lower

rows are equal in length and only slightly shorter than the upper rows; the first lower row is interrupted medially. The fifth, sixth, and seventh (if present) lower rows have decreasing lengths. In many tadpoles the seventh lower tooth row is absent or fragmentary (fig. 261C).

The top of the head and the tip of the snout are brown; the venter is creamy gray. The caudal musculature is tan, and the caudal fin is transparent. A faint creamy, narrow, crescent-shaped mark is present on the posterior edge of the body in most specimens, but it is not bordered posteriorly by a dark brown mark. Dark brown flecks are scattered on the caudal musculature and the caudal fin with the exception of the anterior one-half of the ventral fin. In life the eye is bronze.

**MATING CALL:** The call of *Ptychohyla spinipollex* consists of a single note, "wraack," repeated at intervals of 45 seconds to four minutes. Each note has a duration of about 0.46 seconds and about 147 pulses per second. The dominant frequency is 4300 cycles per second (pl. 31, fig. 3).

**NATURAL HISTORY:** This species occurs in cloud forests and mixed pine and broad-leaved forests, where the frogs breed in cascading mountain streams. Calling males are found on bushes and trees along the streams, and tadpoles have been found in the streams, where they occur primarily in shallow gravel-bottomed pools or in riffles. Two recently metamorphosed young have snout-vent lengths of 15.0 and 15.5 mm.

**REMARKS:** Duellman (1963c) and Lynch and Fugler (1965) mentioned that Guatemalan specimens differ from those in Honduras by having a heavily spotted venter. When I reviewed the genus *Ptychohyla* in 1963, I had not seen living specimens from Honduras and was reluctant to recognize taxonomically the Guatemalan population. I have now seen living individuals from Cerro Uyuea, Honduras; the differences in coloration have been described in the preceding description of this species. Nonetheless, I am still reluctant to recognize taxonomically the Guatemalan specimens, until information is available concerning the tadpoles and the mating call of the frogs in Honduras. Perhaps the Guatemalan populations here re-

ferred to as *Ptychohyla spinipollex* actually represent a distinct species. At the present time, only a few specimens from widely scattered localities are available from Honduras.

**ETYMOLOGY:** The specific name *spinipollex* is derived from the Latin *spina* meaning thorn and the Latin *pollex* meaning thumb and alludes to the spinous nuptial excrescences in breeding males.

**DISTRIBUTION:** *Ptychohyla spinipollex* inhabits cloud forests at elevations of 800 to 1850 meters on the Atlantic slopes of the highlands in Nuclear Central America from the Sierra de los Cuchumatanes in western Guatemala southeastward to north-central Nicaragua (fig. 264).

See Appendix 1 for the locality records of the 67 specimens examined.

### Genus *Plectrohyla* Brocchi

*Plectrohyla* Brocchi, 1877a, p. 92 [type species by original designation, *Plectrohyla guatemalensis* Brocchi, 1877a].

*Cauphias* Brocchi, 1877b, p. 129 [substitute name for *Plectrohyla* Brocchi, 1877a].

**GENEROTYPE:** *Plectrohyla guatemalensis* Brocchi, 1877a, by original designation. Hartweg (1941, p. 1) discussed the generic allocation of Brocchi's names:

"The generic and specific descriptions of *Plectrohyla guatemalensis*, a batrachian from Patzicia, Guatemala, were formulated by Brocchi (1877:92). In the course of his study he discovered another new species which he believed to be closely related to *guatemalensis*. Deciding that the original description of *Plectrohyla* was not satisfactory for the inclusion of both species (*guatemalensis* and the new one), he described a new genus, *Cauphias*, and synonymized *Plectrohyla* with it (1877:129). In the same article (p. 130) he also described his new species, *crassus*. The species *guatemalensis* is the haplotype [monotype] of *Plectrohyla* (Brocchi, 1877:92); Barbour (1927:96) designated *Plectrohyla guatemalensis* as the genotype of *Cauphias*. Although it cannot be definitely shown that the actual publication date of the description of *Plectrohyla* preceded that of *Cauphias*, it seems best to assume so; I therefore regard the names *Cauphias* and *Plectrohyla* as synonyms and select *Plectrohyla* as



the proper name to be used. Should future researches show that *crassus* (*crassum*), is generically distinct, the name *Cauphias* may not be resurrected, since it is a synonym of *Plectrohyla*."

Hartweg's assumption that the description of *Plectrohyla* antedates that of *Cauphias* is logical, because both names were published in the Bulletin de la Société Philomathique de Paris (Series 7, volume 1). The description of *Plectrohyla* is on page 92 in number 2, and that of *Cauphias* is on page 129 in number 3. Duellman (1964b, p. 488) showed that *Cauphias crassus* is actually a member of the *Hyla bistincta* group.

**ETYMOLOGY:** The generic name is derived from the Greek *plektron*, meaning spur, and *Hylas*, a character in Greek mythology. The generic name is in reference to the prepollical spines, characteristic of members of the genus.

**DEFINITION:** Frogs of the genus *Plectrohyla* are moderately small to large in size; they are variously colored but usually have a green, gray, or brown dorsum and lack bright markings. The pupil is horizontal, and the palpebral membrane is clear. The fingers and toes are long and bear moderately large discs. The webbing on the hands is vestigial, whereas that on the feet is extensive. Individuals of both sexes have an enlarged prepollex that is supported internally by a large bony element, the prepollical spine or process; the spine protrudes through the skin in some species. Vocal slits and a single, median, subgular vocal sac are present in males of four species and absent in the others. The skin on the dorsum is thick and glandular; it is smooth in some species but tuberculate in most. There is no integumentary-cranial co-ossification. The lips are thickened and the forearms are hypertrophied in breeding males of some species.

The skull is broad and moderately shallow. The skull is characterized by a frontoparietal fontanelle, a well-ossified sphenethmoid, and relatively small nasals, which in most species are separated medially and bear a slender maxillary process that articulates with the well-developed posterior process of the pars facialis of the maxillary (fig. 266). The squamosal is robust, and the anterior arm does not

extend to the maxillary. The pterygoid is robust, and the median ramus of the pterygoid is in bony contact with the prootic. The quadratojugal is absent or reduced to a small spur posteriorly. The maxillary and premaxillary are robust. An apparently unique condition of the premaxillaries distinguishes this genus. The alary process of the premaxillary is bifurcate posteriorly. The dorsal tip of the alary process lies adjacent to the nasal cartilages anteroventral to the nasals. The posterior ramus of the alary process extends beneath the anterior part of the sphenethmoid (fig. 18A). Thus, the premaxillaries and alary processes support the entire nasal region and anterior end of the sphenethmoid. Teeth are present on the premaxillaries, maxillaries, and prevomers, whereas the palatines and parasphenoid are edentate. The teeth are blunt and weakly bifid or long and pointed (fig. 267).

The known tadpoles are stream inhabitants with robust bodies and long muscular tails with low fins. The mouth is ventral and completely bordered by papillae but lacks lateral folds. There are two upper and three lower rows of teeth that are relatively short. The mating call consists of a single quack-like note or a series of short notes. The haploid number of chromosomes is 12 (known only in *ixil* and *sagorum*).

**COMPOSITION OF GENUS:** Ten monotypic species are recognized in the genus, which is endemic to the highlands of Nuclear Central America. Of these species, 584 preserved frogs, 22 skeletons, and 57 lots of tadpoles have been examined.

**ANALYSIS OF CHARACTERS:** *Plectrohyla avia* is the largest species and *matudai* is the smallest; males of the former attain snout-vent lengths of 90 mm., and, of the latter, 36 mm. Females of the small species (*ixil*, *matudai*, *quechchi*, and *sagorum*) are somewhat larger than the males, whereas in the larger species the females, if known, are about the same size as the males. The sizes and proportions of the ten species are summarized in table 53.

The taxonomically important external characters are those of the skin, shape of the snout, and nature of the prepollical spine. *Plectrohyla guatemalensis*, *hartwegi*, *matudai*, *pynochila*, and *sagorum* have numerous and

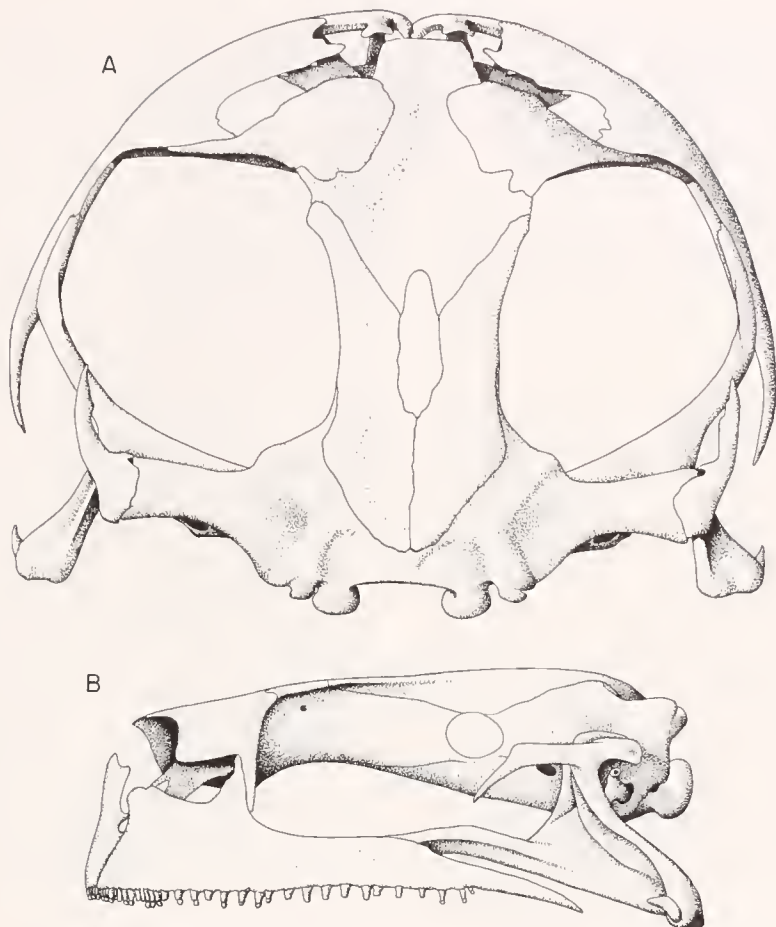


FIG. 266. Dorsal (A) and lateral (B) views of the skull of *Plectrohyla guatemalensis*, K.U. No. 68664.  $\times 6$ .

conspicuous tubercles on the dorsum, whereas the skin in the other species is relatively smooth (some have scattered low tubercles), except in *avia*, which has tubercles on the head. The snout is bluntly rounded in *avia*, *guatemalensis*, *hartwegi*, *pynochila*, and *quecchi*, truncate in *matudai* and acuminate in the other species. A narrow, fleshy, vertical rostral keel is present in *quecchi* and *sagorum*. Adults of both sexes have bony prepollical processes; these usually are better developed in males than in females. In some males, the spine actually protrudes through the skin. The shape of the prepollical process is one of the most useful taxonomic characters in this genus, and the shape varies from a flat plate or elongate, rounded blunt spur to a simple curved spine or bifid spine (fig. 268).

The fingers of all species are long and bear moderately large discs. The feet are moderately well webbed and have large sub-articular tubercles (figs. 269-273). A strong inner tarsal fold is present in all species, and a distinct outer tarsal fold is present in some populations of *P. glandulosa*.

The arms of breeding males are greatly hypertrophied, and in some breeding males the lips are swollen. No histological examination of the lips has been made, but examination of the hypertrophied arms revealed that there was no modification, other than extreme muscular development in several species (*glandulosa*, *guatemalensis*, *ixil*, *matudai*, *quecchi*, and *sagorum*), but that in *avia* the humerus is greatly modified (fig. 274). The humerus is massive with well-developed

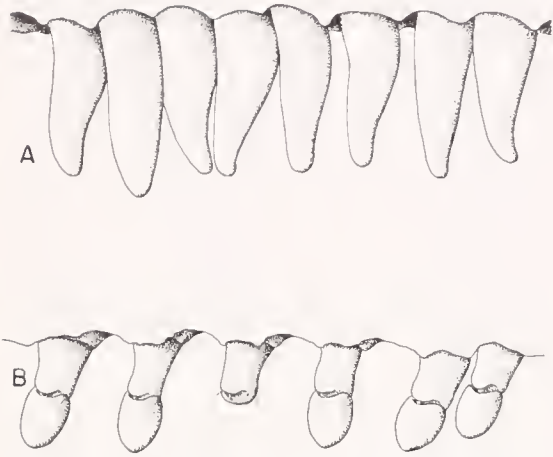


FIG. 267. Lateral view of maxillary teeth. A. *Plectrohyla avia*, K.U. No. 106295. B. *Plectrohyla guatemalensis*, K.U. No. 68664.  $\times 20$ .

ridges. The crista ventralis begins on the capitulum and continues as a heavy, moderately deep ridge for about 40 per cent of the length of the humerus. The crista medialis is greatly expanded on the distal half of the humerus. The crista lateralis extends for two-thirds of the length of the bone. A broad, deep, V-shaped depression exists between the crista medialis and the crista lateralis.

Linea masculinea are present in *P. ixil* and *matudai* and apparently absent in other species. The skin of *P. glandulosa* contains a layer of melanin; presumably this is an adaptation protecting the internal organs from solar radiation in this species which frequently basks on rocks and clumps of grass.

The teeth in four species (*avia*, *glandulosa*, *lacertosa*, and *sagorum*) are pointed; in the others the teeth are barely spatulate and not, or only weakly, bifid (fig. 267). There is considerable variation in the number of teeth (table 54). In most groups of related species of hylids the larger species have more teeth than do the smaller species, but in *Plectrohyla*, this is not the case, the smallest species (*matudai*) has more teeth than any of the three largest species (*avia*, *guatemalensis*, and *hartwegi*).

The tadpoles of six species are known. Of these, the tadpoles of *P. guatemalensis* are different in having two rows of papillae bordering the mouth and blunt peg-like serrations on the beaks. The tadpoles of *guatemalensis* and *glandulosa* are alike in having robust bodies and heavy wrinkled skin (fig. 275), but *glandulosa* differs by having one row of fringing papillae; in this respect, it is like the other known tadpoles (table 55). The tadpoles of *matudai* and *ixil* are unique by

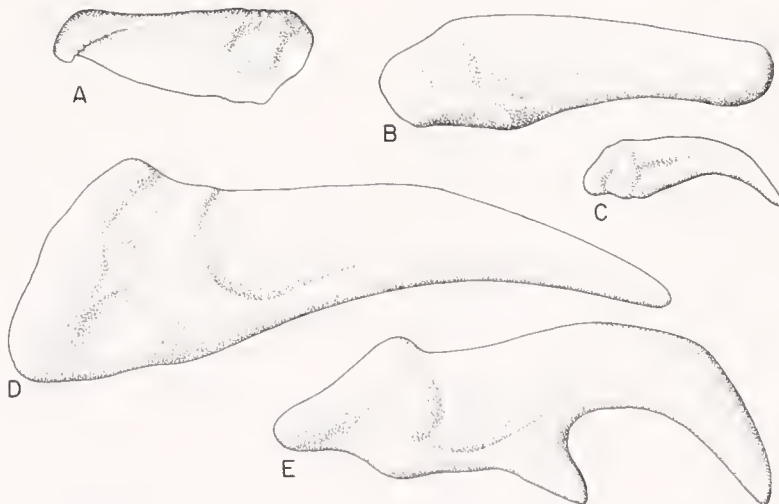


FIG. 268. Prepollical processes of *Plectrohyla* (palmar view of right hand). A. *P. glandulosa*, K.U. No. 59828 (same in *pycnochila*). B. *P. lacertosa*, U.I.M.N.H. No. 33693. C. *P. ixil*, K.U. No. 59834 (same in *matudai*, *quecchi*, and *sagorum*). D. *P. avia*, K.U. No. 106295. E. *P. guatemalensis*, K.U. No. 68664 (same in *hartwegi*).  $\times 10$ .



TABLE 53  
Comparison of Sizes (in Millimeters) and Certain Proportions, with Means  
in Parentheses, of Adult Males of the Species of *Plectrohyla*.

Species	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
<i>P. matudai</i>	8	31.5-35.6 (33.1)	0.496-0.540 (0.509)	0.375-0.444 (0.412)	0.334-0.382 (0.355)	0.341-0.460 (0.392)	0.400-0.575 (0.495)
<i>P. ixil</i>	22	36.9-41.6 (38.9)	0.468-0.529 (0.499)	0.412-0.462 (0.438)	0.286-0.369 (0.332)	0.331-0.395 (0.355)	0.365-0.510 (0.440)
<i>P. sagorum</i>	15	33.6-45.5 (39.3)	0.462-0.591 (0.520)	0.392-0.484 (0.438)	0.285-0.346 (0.315)	0.308-0.385 (0.350)	0.333-0.719 (0.496)
<i>P. quecchi</i>	8	40.4-43.8 (42.2)	0.514-0.554 (0.531)	0.460-0.493 (0.480)	0.294-0.338 (0.318)	0.342-0.390 (0.368)	0.346-0.463 (0.411)
<i>P. glandulosa</i>	12	42.2-49.1 (44.6)	0.471-0.543 (0.513)	0.462-0.524 (0.480)	0.274-0.321 (0.296)	0.323-0.394 (0.352)	0.255-0.537 (0.375)
<i>P. pycnophila</i>	2	52.5-60.5 (56.5)	0.502-0.581 (0.542)	0.463-0.530 (0.497)	0.288	0.332-0.347 (0.352)	0.464-0.484 (0.474)
<i>P. lacertosa</i>	1	47.8	0.494	0.460	0.310	0.366	.....
<i>P. avia</i>	4	82.5-90.4 (86.2)	0.483-0.532 (0.509)	0.470-0.487 (0.478)	0.317-0.335 (0.323)	0.354-0.356 (0.355)	0.397-0.543 (0.468)
<i>P. gnatemalensis</i>	20	51.2-76.1 (64.0)	0.486-0.576 (0.531)	0.407-0.513 (0.465)	0.255-0.305 (0.286)	0.291-0.347 (0.335)	0.240-0.373 (0.329)
<i>P. hartwegi</i>	3	41.8-63.8 (51.3)	0.547-0.579 (0.558)	0.464-0.487 (0.475)	0.309-0.339 (0.322)	0.350-0.377 (0.360)	0.426-0.473 (0.445)

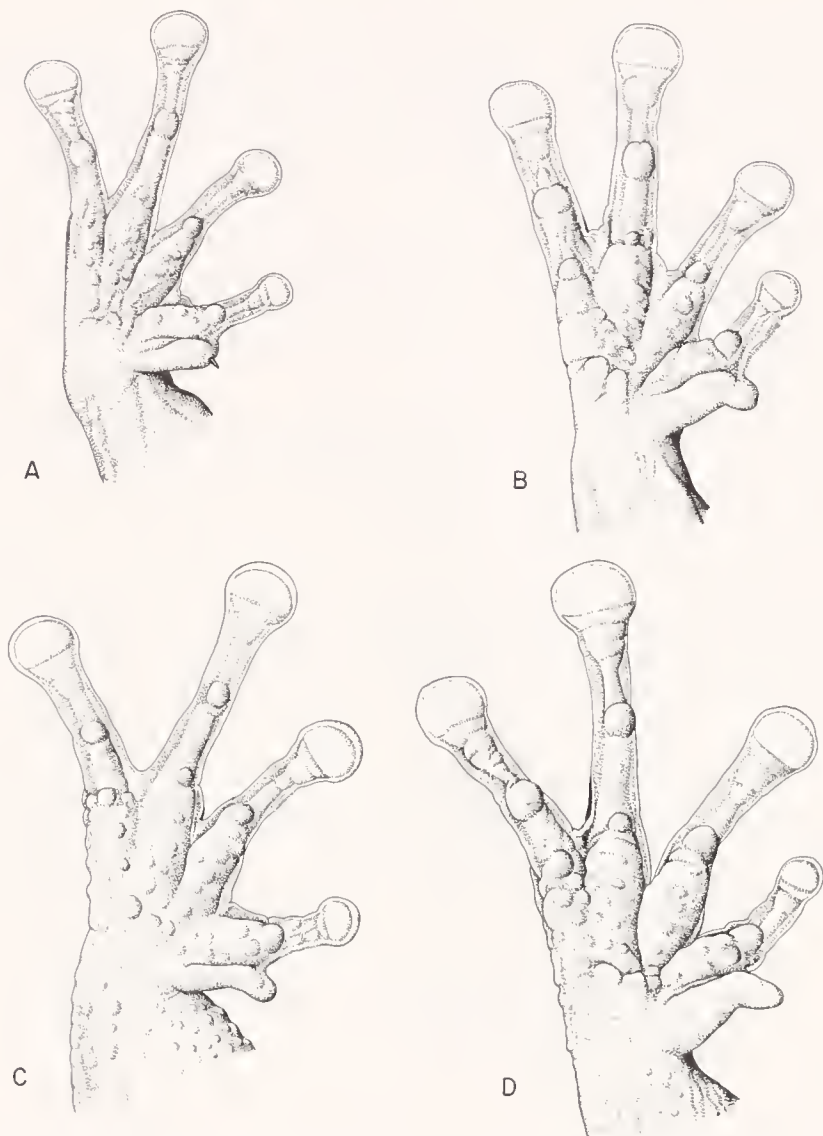


FIG. 269. Hands of four species of *Plectrohyla*. A. *P. matudai*, K.U. No. 58869. B. *P. ixil*, K.U. No. 58854. C. *P. sagorum*, K.U. No. 103164. D. *P. quecchi*, K.U. No. 64115.  $\times 4$ .

having unequal serrations on the upper beak. In *ixil* two or three serrations on either side are noticeably enlarged, whereas in *matudai* one serration is enlarged and fang-like on either side. The serrations are subequal in the other species (fig. 276).

**DISTRIBUTION:** Frogs of the genus *Plectrohyla* occur at moderate to high elevations (1000 to 3500 meters) in the highlands of northern Central America (Honduras, El Salvador, Guatemala, and the states of Chiapas

and Oaxaca, México). Ecologically the species inhabit montane meadows, pine-cypress forest, pine-oak forest, and cloud forest. All presumably are stream-breeders.

**DISCUSSION:** The members of the genus fall into two seemingly natural groups: 1) Small species having vocal slits (*ixil*, *matudai*, *quecchi*, and *sagorum*). 2) Medium-sized to large species lacking vocal slits (*avia*, *glandulosa*, *guatemalensis*, *hartwegi*, *lancertosa*, and *pynochila*).

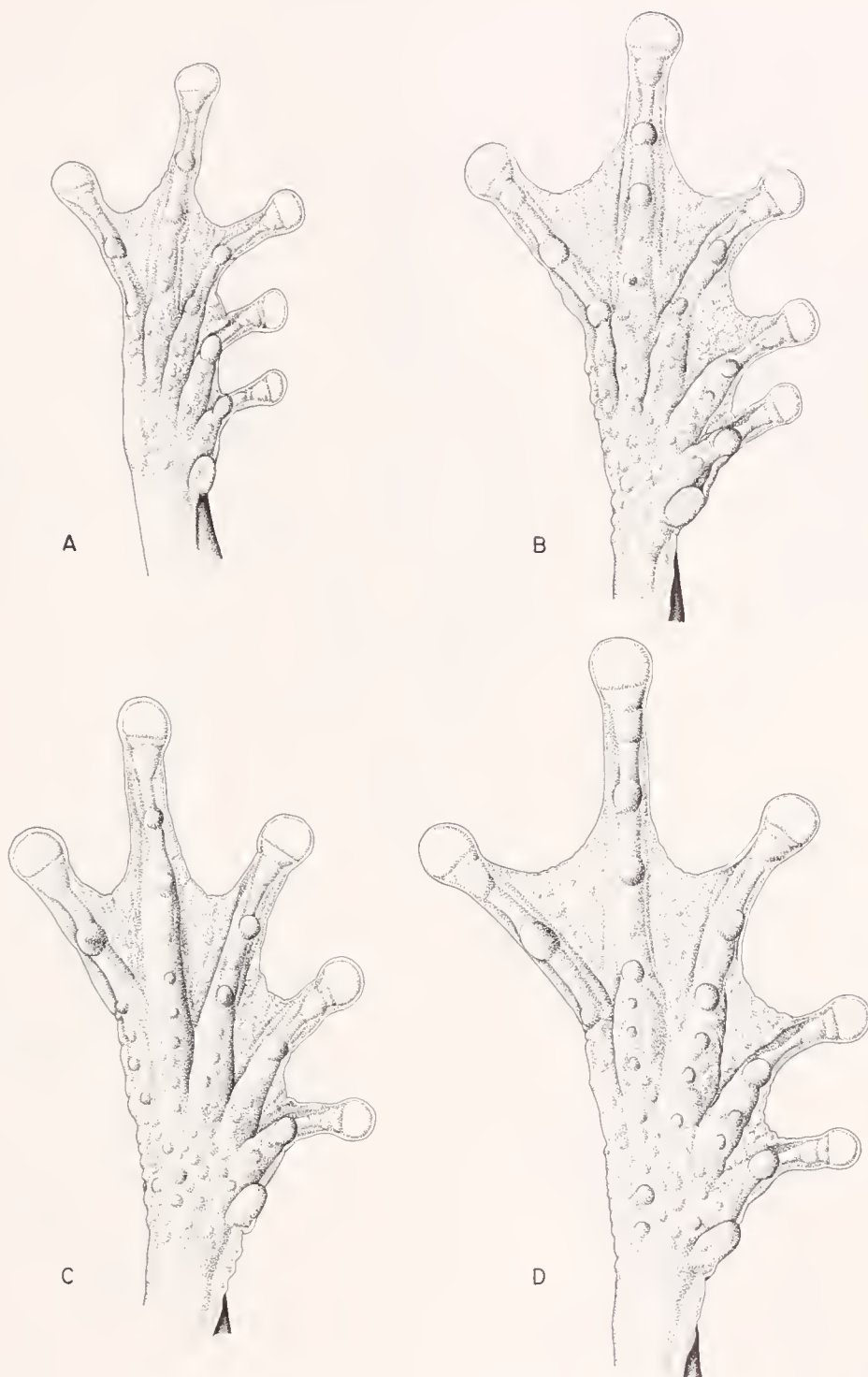


FIG. 270. Feet of four species of *Plectrohyla*. A. *P. matudai*, K.U. No. 58869. B. *P. ixil*, K.U. No. 58854. C. *P. sagorum*, K.U. No. 193164. D. *P. quecchi*, K.U. No. 64115.  $\times 3.5$ .





FIG. 271. Hands of three species of *Plectrohyla*. B. *P. lacertosa*, U.I.M.N.H. 33693. C. *P. glandulosa*, K.U. No. 58708. A. *P. pycnochila*, T.C.W.C. No. 21459.  $\times 4$ .

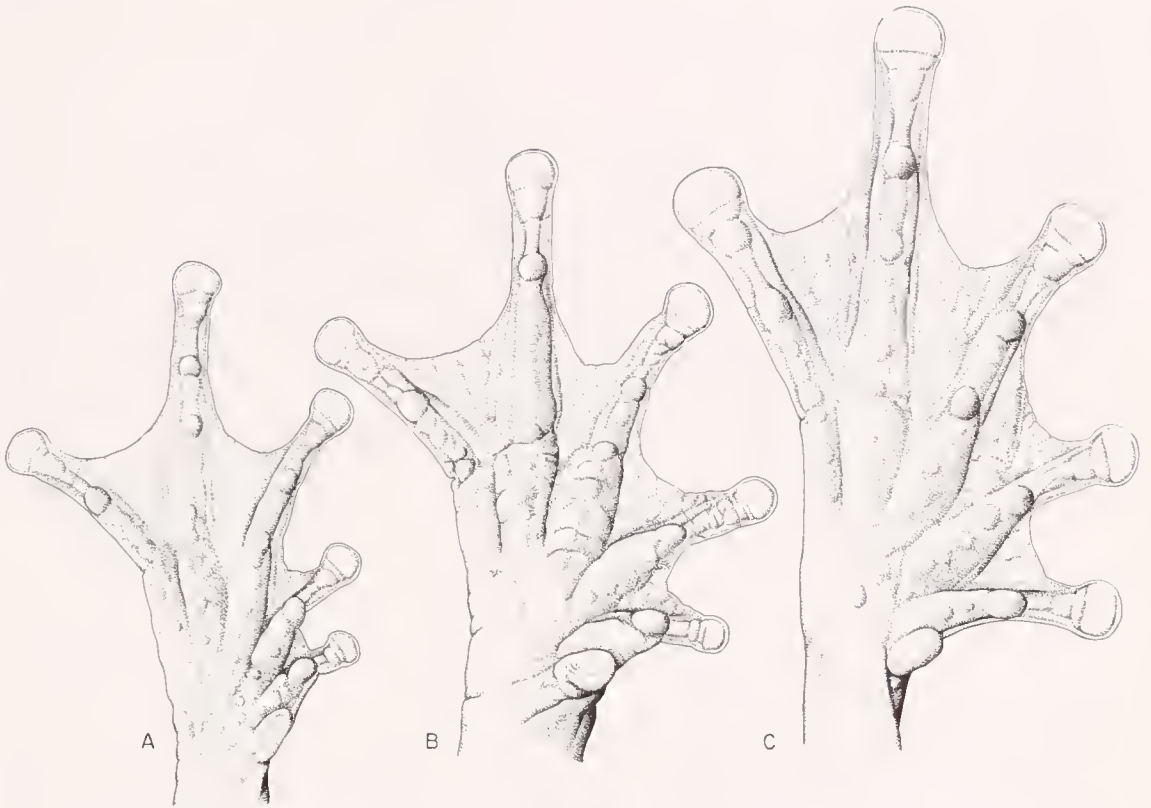


FIG. 272. Feet of three species of *Plectrohyla*. A. *P. glandulosa*, K.U. No. 58708. B. *P. lacertosa*, U.I.M.N.H. No. 33693. C. *P. pycnochila*, T.C.W.C. No. 21459.  $\times 3$ .

*Plectrohyla* apparently is closely related to the *Hyla bistincta* group in the Mexican highlands northwest of the Isthmus of Tehuantepec. Probably *Plectrohyla* and the *Hyla bistincta* group evolved from a common ancestor. The members of both groups show parallel adaptations to the lotic environment; some members of each group have lost the voice. Since the *Hyla bistincta* group has evolved in the Mexican highlands, it is only logical to assume that the ancestral stock that gave rise to *Plectrohyla* was isolated in northern Central America.

The *Plectrohyla* stock probably was in the area this is now Chiapas and Guatemala in the Miocene prior to the uplift of Nuclear Central America that began in the Pliocene. Conceivably, in the course of uplift, the *Plectrohyla* stock was separated into a highland component and another component at moderate elevations on the slopes. The latter

component retained vocal slits and evolved into a group of small species, whereas the highland component evolved into a group of larger species lacking vocal slits.

The former group, which for convenience can be called the *sagorum* group, eventually established populations on the Atlantic and Pacific slopes of the highlands. Possibly, the species now known as *quecchi* was the original inhabitant on the Atlantic slopes, whereas *matudai* was endemic to the Pacific slopes. Through isolation differences in voice, shape of the snout, and mouthparts of the tadpoles developed. Subsequent climatic fluctuation, probably in the Pleistocene, permitted migration southward of the *quecchi*-stock and northward of the *matudai*-stock. Depression of climatic zones and uplift through volcanism again resulted in isolation of populations on Atlantic and Pacific slopes, but this time two species were present on each slope. The



FIG. 273. Hands and feet of three species of *Plectrohyla*. A and D. *P. avia*, K.U. No. 94016. B and E. *P. guatemalensis*, K.U. No. 64102. C. and F. *P. hartwegi*, U.M.M.Z. No. 94428.  $\times 2$ .





FIG. 274. Posterolateral view of the left humerus of *Plectrohyla avia*, K.U. No. 106295. CL=crista lateralis, CM=crista medialis, CV=crista ventralis,  $\times$  3.

*matudai*-stock on the Atlantic slope differentiated into *ixil*, and the *quecchi*-stock on the Pacific slope evolved into *sagorum*.

This close relationship between *sagorum* and *quecchi* and between *ixil* and *matudai* are obvious on the basis of morphological characters of the adults and tadpoles and in the similarities of the mating calls. Conceivably, *matudai* and *ixil* are subspecifically related, and possibly *sagorum* and *quecchi* are conspecific. Because each nominate species possesses a distinctive combination of morphological characters, in the absence of biological evidence to support a closer relationship, the four populations are regarded herein as distinct species.

The relationships of the species in the highland component (*guatemalensis* group) are more obscure, because tadpoles are unknown for four species, and the absence of a voice precludes the use of that taxonomically useful trait. *Plectrohyla glandulosa* and *pynochila* seem to be the least specialized species; the condition of the prepollical process in these species probably is relatively unchanged from that of the *Plectrohyla* prototype and is much like that in the *Hyla bistincta* group. It is possible that *glandulosa*

TABLE 54  
Dentitional Characteristics of the Species of *Plectrohyla*.

Species	Shape	Number of Teeth <sup>a</sup>	
		Prevo- merine	Maxillary- Premaxillary
<i>P. matudai</i> .....	Spatulate	3-5	50-61
<i>P. ixil</i> .....	Spatulate	3-5	41-58
<i>P. sagorum</i> .....	Pointed	3-4	34-45
<i>P. quecchi</i> .....	Spatulate	3-4	47-53
<i>P. glandulosa</i> .....	Pointed	1-3	23-30
<i>P. pynochila</i> .....	Spatulate	3-5	31-36
<i>P. lacertosa</i> .....	Pointed	2-3	30-31
<i>P. avia</i> .....	Pointed	1-3	27-33
<i>P. guatemalen-</i> <i>sis</i> .....	Spatulate	3-6	32-39
<i>P. hartwegi</i> .....	Spatulate	4-5	35-40

<sup>a</sup> One side only.

developed in the Sierra de Cuchumatanes in Guatemala while *pynochila* was isolated in the highlands of central Chiapas.

Apparently *Plectrohyla avia* represents an evolutionary intermediary between the generalized *glandulosa*-*pynochila* stock and *guatemalensis* and *hartwegi*. The prepollical spine is long and pointed in *avia* (independently evolved in the *sagorum* group) and is bifid in *guatemalensis* and *hartwegi*. *Plectrohyla avia* is endemic to moderately high elevations on the Pacific slopes; *hartwegi* occurs at the same elevations but farther west. *Plectrohyla guatemalensis* occurs nearly throughout the geographical (but not the altitudinal) range of the genus. It occurs sympatrically with *avia* and possibly with *hartwegi*. The complicated paleogeography and climatic history of Nuclear Central America undoubtedly provided several barriers resulting in the isolation of populations which evolved into the three species and provided the physical basis for their present distributions.

*Plectrohyla lacertosa* is known to science solely by one miserably preserved adult male lacking specific locality data. Indeed, it is unfortunate that the specimen possesses such a distinctive combination of characters that it cannot be relegated to the synonymy of another species. This moderate-sized species with a unique prepollical process lacks vocal slits and thereby seems to belong in the

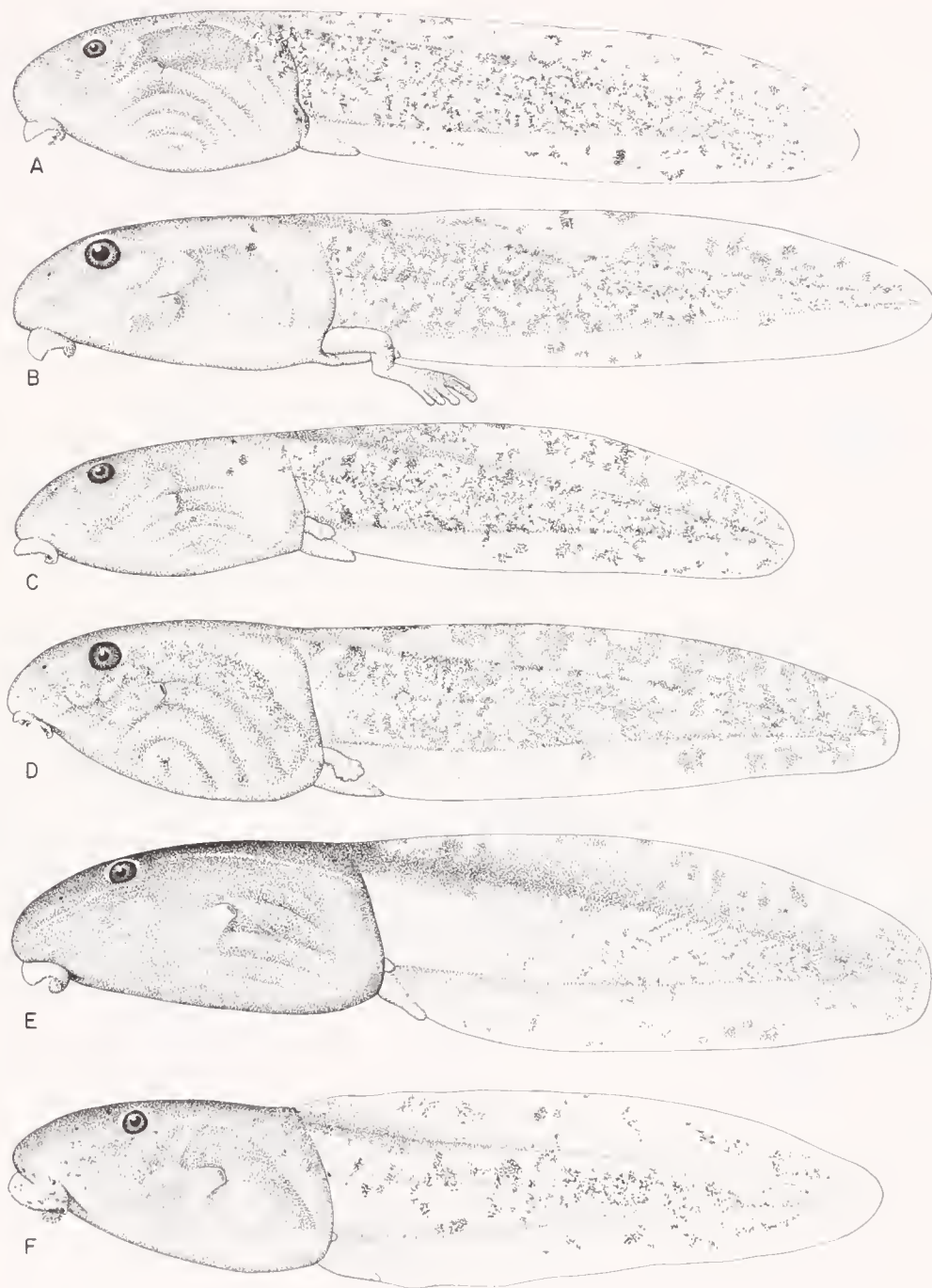


FIG. 275. Tadpoles of six species of *Plectrohyla*. A. *P. matudai*, K.U. No. 60036. B. *P. ixil*, K.U. No. 60034. C. *P. sagorum*, K.U. No. 104195. D. *P. quecchi*, K.U. No. 60038. E. *P. glandulosa*, K.U. No. 104193. F. *P. guatemalensis*, K.U. No. 60033.  $\times 3$ .

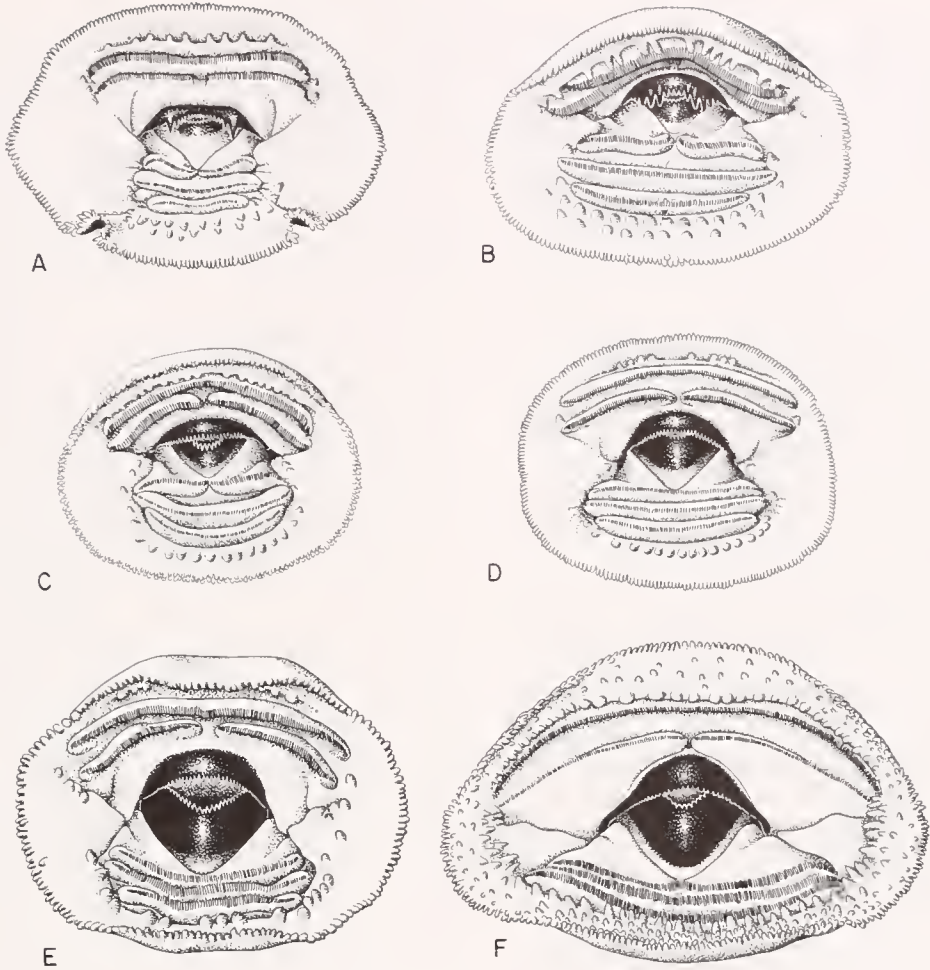


FIG. 276. Mouths of tadpoles of six species of *Plectrohyla*. A. *P. matudai*, K.U. No. 60036. B. *P. ixil*, K.U. No. 60034. C. *P. sagorum*, K.U. No. 104195. D. *P. quecchi*, K.U. No. 60038. E. *P. glandulosa*, K.U. No. 104193. F. *P. guatemalensis*, K.U. No. 60033.  $\times 10$ .

*guatemalensis* group. Until more material is available nothing further can be ascertained about its relationships.

#### *Plectrohyla matudai* Hartweg

*Plectrohyla matudai* Hartweg, 1941, p. 5 [holotype, U.M.M.Z. No. 88863 from Cerro Ovando, Distrito Soconusco, Chiapas, México, elevation 1800 meters; Norman Hartweg collector]. Smith and Taylor, 1948, p. 73. Lynch and Smith, 1966, p. 62 [synonymized *Plectrohyla brachycephala* Taylor, 1949b, with *P. matudai* Hartweg, 1941].

*Plectrohyla brachycephala* Taylor, 1949b, p. 16 [holotype, A.M.N.H. No. 53761 from a tributary of the Río Ostuta, at the foot of the Sierra Madre between Sierra Madre and Cerro Atravesado, Oaxaca, México; Thomas C. MacDougall collector].

*Plectrohyla matudai brachycephala*: Bumzahem and Smith, 1954, p. 62.

*Plectrohyla matudai matudai*: Bumzahem and Smith, 1954, p. 62. Stuart, 1963, p. 40.

**DIAGNOSIS:** This small species (37 mm. in snout-vent length) has a tuberculate dorsum, a blunt snout, and vocal slits. The prepollical spine is long and pointed. The dorsal coloration is separated from that on the venter by a dark line or irregular row of small spots. *Plectrohyla ixil* has a less tuberculate or smooth dorsum, an acuminate snout, and usually a lateral light stripe. *Plectrohyla quecchi* and *sagorum* have a vertical rostral keel. The other members of the genus are larger and lack vocal slits.



TABLE 55  
Comparison of Certain Features in the Known Tadpoles in *Plectrohyla*.

Species	Rows of Fringing Papillae	Papillae Lateral to Beaks	Upper Tooth Rows	Lower Tooth Rows	Serrations on Beak
<i>P. matudai</i> .....	One; larger papillae medially	Very few	Moderately long	Third much shorter	Pointed; two fang-like on upper
<i>P. ixil</i> .....	One; larger papillae medially	Few, scattered	Moderately long	Third shorter	Pointed; some enlarged on upper
<i>P. sagorum</i> .....	One; larger papillae medially	Few	Moderately long	Third shorter	Pointed; subequal on upper
<i>P. quecchi</i> .....	One; larger papillae medially	None	Moderately long	Third shorter	Pointed; subequal on upper
<i>P. glandulosa</i> .....	One; row of larger papillae medially	None	Moderately long	Third much shorter	Pointed; subequal on upper
<i>P. guatemalensis</i> .....	Two; row of larger papillae medially	Many	Long	Subequal	Blunt; subequal on upper

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 46.0 mm., and females reach 49.0 mm. In a series of eight males from Finca La Paz, Departamento San Marcos, Guatemala, the snout-vent length is 31.5 to 35.6 (mean, 33.1) mm.; the ratio of tibia length to snout-vent length is 0.496 to 0.540 (mean, 0.509); the ratio of foot length to snout-vent length is 0.375 to 0.444 (mean, 0.412); the ratio of head length to snout-vent length is 0.334 to 0.382 (mean, 0.355); the ratio of head width to snout-vent length is 0.341 to 0.460 (mean, 0.392), and the ratio of the diameter of the tympanum to that of the eye is 0.400 to 0.575 (mean, 0.495). Specimens from the western part of the range apparently attain a larger size. Bumzahem and Smith (1954, p. 63) reported that the snout-vent length of nine males from Región de Soconusco, Chiapas, México, was 36 to 46 mm.; Taylor (1949b, p. 19) reported snout-vent lengths of 35.0 to 40.0 mm. in four specimens from the Río Ostuta, Oaxaca, México.

The head is as wide as the body, and the top of the head is flat; the snout is truncate in dorsal and lateral profiles; the snout is short, and its length is equal to the diameter of the eye. The nostrils are protuberant, di-

rected dorsolaterally, and situated at the terminus of the snout. The canthus is slightly elevated and sharply angular, and the loreal region is nearly flat. The lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum; the posterior edge of the tympanum is indistinct in most specimens, whereas the anterior and ventral edges of the tympanum usually are well defined. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately short and robust; they are swollen in some breeding males. A longitudinal row of tubercles is present on the ventrolateral edge of the forearm, and a transverse dermal fold is present on the wrist. The fingers are long and slender, and bear moderately large discs; the width of the disc on the third finger is greater than the diameter of the tympanum. The subarticular tubercles are large and conical; the distal tubercles on the third and fourth fingers are bifid in some individuals. The supernumerary

tubercles are large and subconical; usually they are present in a single row on the proximal segment of the first and fourth fingers and in two rows on the proximal segments of the second and third fingers. An elevated, bifid palmar tubercle is present. The prepollex is moderately enlarged and terminally curved; in some males, the sharp prepollical spine protrudes from the terminus of the prepollex. The webbing on the hand is vestigial (fig. 269A). The legs are relatively short; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the eye. A few small tubercles are present on the heel, but there is no transverse dermal fold. An elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is ovoid and subconical; no distinct outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately small and conical; the supernumerary tubercles are moderately large, subconical, and arranged in a single row on each digit, except proximally the arrangement breaks down so that the tubercles are irregularly placed. The toes are about three-fourths webbed (fig. 270A). The webbing extends from the base of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally at the midlevel of the thighs. A short, broad anal sheath is bordered on either side by a moderately large tubercle. The skin on the dorsum is tuberculate; tubercles are present on the flanks. The skin on the throat, belly, and ventral surfaces of the thighs is coarsely granular, and that on the other ven- tral surfaces is smooth. The tongue is elon- gatedly cordiform, distinctly notched posterior- ly, barely free behind, and in some specimens shallowly notched anteriorly. The dentigerous processes of the prevomers are widely separated, transverse elevations between the

posterior margins of the moderately small ovoid choanae. Three to five teeth are pres- ent on each elevation. The number of teeth on the maxillary and premaxillary (one side only) varies from 50 to 61. The vocal slit extends from the midlateral base of the tongue to the angle of the jaws. The vocal sae is single, median, subgular, and only mod- erately distensible.

The general coloration of *Plectrohyla ma- tudai* is tan or brown with darker brown ir- regular spots or reticulations on the dorsum (pl. 68, fig. 1). In most individuals, the dor- sum is pale brown with dark brown, olive- brown, or black flecks and/or bold reticula- tions on the back. Narrow, dark bars or series of flecks are present on the dorsal sur- faces of the limbs. Most individuals have a narrow dark vertical bar on the upper lip, below the eye. In most individuals, a dark, irregular stripe, which may be fragmented into a series of dashes or flecks, extends from the supratympanic fold nearly to the groin. The stripe or flecks separate the brown dor- sal color from the creamy tan on the flanks. In some individuals, the narrow dark stripe is absent. The axilla usually is gray or bluish gray, and this color usually is narrowly out- lined with black. A few black flecks are pres- ent on the flanks. The anterior surfaces of the thighs are creamy tan, and the posterior surfaces of the thighs are pale brown. The venter is creamy white, and the vocal sae is grayish brown. The iris is coppery tan with fine black reticulations. In some specimens, minute, metallic green flecks are scattered on the dorsal surfaces.

In preservative, the dorsum is dull brown with darker brown or black markings. The anterior and posterior surfaces of the thighs are pale tan or brown, and the venter is creamy tan or pale grayish brown.

**TADPOLES:** Five tadpoles in developmen- tal stage 25 from Finca La Paz, Departamento San Marcos, Guatemala, have body lengths of 10.5 to 13.1 (mean, 11.6) mm. and total lengths of 29.5 to 38.2 (mean, 33.5) mm. A typical tadpole in developmental stage 28 from the same locality has a body length of 13.7 mm. and a total length of 40.5 mm. In dorsal profile, the body is ovoid; the body is slightly wider than deep and not noticeably

depressed. In dorsal profile the snout is bluntly rounded and in lateral profile, truncate. The eyes are small and directed dorso-laterally. The nostrils are situated about midway between the eyes and the tip of the snout and are directed anterolaterally. The opening of the sinistral spiracle is about on the midline about midway on the length of the body. The cloacal tube is long and dextral. The caudal musculature is heavy and extends nearly to the tip of the rounded tail. The caudal fins are shallow; the dorsal fin is deepest at a point slightly posterior to the midlength of the tail. Throughout its length, the dorsal fin is deeper than the ventral and the dorsal fin does not extend onto the body. At midlength of the tail, the depth of the caudal musculature is much greater than the depth of either fin (fig. 275A).

The body is brown, and the caudal musculature is tan with dark reddish brown flecks. Similarly colored flecks are present on the caudal fins. The iris is dull bronze. In preservative, the body is dull brown or grayish brown, and the caudal musculature is pinkish tan with brown flecks.

The mouth is ventral and moderately large; it is equal to two-thirds of the width of the body. The mouth is completely bordered by a single row of small papillae. Medial to these there is an irregular row of larger papillae. The upper beak is broad and barely arched. Moderately long, pointed serrations are present on the beak; one serration on either side is greatly enlarged into a fang-like projection. The lower beak is narrow and forms a broad, curved arch; it bears small, pointed serrations. There are two upper and three lower rows of teeth. The upper rows are long and equal in length; the second upper row is narrowly interrupted medially. The first and second lower rows are equal in length and noticeably shorter than the upper rows, and the third lower row is shorter than the other lower rows (fig. 276A).

Hartweg and Orton (1941, p. 2) described and illustrated the tadpole of this species under the name "Form a."

**MATING CALL:** Recordings of the call of *Plectrohyla matudai* are not available, but I have heard this species calling at Finca La Paz, Departamento San Marcos, Guatemala.

The call consists of a single note. Taylor and Smith (1945, p. 597) described the call as "a single, sharp note that sounds very much like two pebbles struck together under water. The note is repeated at intervals of about two minutes."

**NATURAL HISTORY:** *Plectrohyla matudai* inhabits pine-oak forest and primarily cloud forest, where the species lives along small cascading streams. Individuals have been found on vegetation along the streams both by day and night. Taylor and Smith (*loc. cit.*) reported finding the frogs on vegetation and boulders along a stream on Cerro Ovan-do, Chiapas, México; they noted that one male was calling from the water in the stream. All calling males that I have observed were sitting on vegetation.

The tadpoles develop in the streams, where they characteristically are found adhering to boulders in quiet sections of the streams. One recently metamorphosed individual having a snout-vent length of 17.9 mm. was found on a small herb at the edge of a stream at Finca La Paz on July 30, 1960. Throughout much of its range, *Plectrohyla matudai* occurs sympatrically with *P. sagorum* and *guatemalensis*. The latter species usually inhabits the larger mountain streams, whereas *matudai* and *sagorum* occur along small streams and rivulets.

**REMARKS:** Taylor (1949b, p. 16) named *Plectrohyla brachycephala* on the basis of four specimens from the Sierra Madre in extreme eastern Oaxaca, México. In diagnosing his new species, Taylor utilized the following characters: relative concealment of the tympanum, the elevation of the tarsal fold, the relative height of the snout, the relative pustularity of the dorsum, and certain characteristics of coloration. Bumzahem and Smith (1954, p. 63), reported on a specimen from Cerro Baul, Oaxaca (U.I.M.N.H. No. 33835), which they considered to be intermediate between *matudai* and *brachycephala*. They stated: "On the whole, the specimen seems closer to *brachycephala*, but it cannot be regarded as typical of either form. Furthermore, the present specimen was collected in an area intermediate geographically between those to be occupied by *matudai* and *brachycephala*. These facts seem to indicate that



the specimen from Cerro Baul is most reasonably interpreted as an intergrade, and that *brachycephala* should, at least until further data is available, be considered as a subspecies of *Plectrohyla matudai*."

Lynch and Smith (1966, p. 62) reported on 35 specimens from Chiapas and Oaxaca. They concluded that *Plectrohyla brachycephala* was unrecognizable, and they placed the name in the synonymy of *Plectrohyla matudai*.

**ETYMOLOGY:** The specific name is a patronym for Eizi Matuda of Chiapas, México.

**DISTRIBUTION:** *Plectrohyla matudai* occurs at elevations of 1000 to 2300 meters on the Pacific slopes of the Sierra Madre from extreme eastern Oaxaca, México, to central Guatemala; this species also is known from the Grijalva depression in western Guatemala

and from the Las Nubes block in central Guatemala (fig. 277).

See Appendix 1 for the locality records of the 139 specimens examined.

### *Plectrohyla ixil* Stuart

*Plectrohyla ixil* Stuart, 1942, p. 4 [holotype, U.M.M.Z. No. 89092 from Finca San Francisco, 25 kilometers north of Nebaj, El Quiché, Guatemala, elevation 1175 meters; Laurence C. Stuart collector; 1963, p. 39.

**DIAGNOSIS:** This small species (40 mm. in snout-vent length) has vocal slits and a long pointed prepollical spine. The dorsum is weakly tuberculate or smooth, and the snout in dorsal profile is acuminate but lacks a vertical keel. A broad light lateral stripe, bordered below by a dark line separates the dorsal color from that on the venter. *Plectro-*

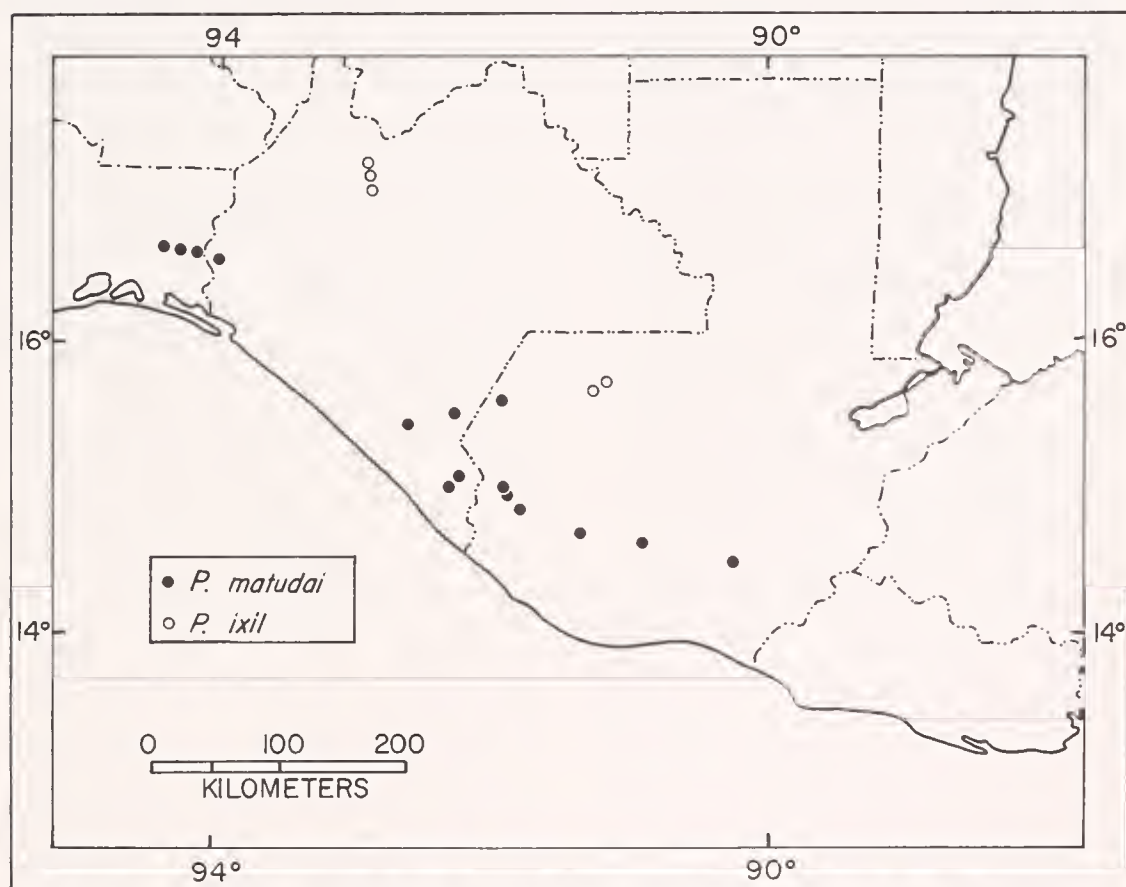


FIG. 277. Distribution of *Plectrohyla matudai* and *Plectrohyla ixil*.

*hyla matudai* differs by having a blunt snout, more tuberculate dorsum, and usually by lacking a lateral light stripe, although a dark line or irregular row of spots is present in most specimens. *Plectrohyla quecchi* and *sagorum* have a vertical rostral keel, and all other members of the genus are larger and lack vocal slits.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 41.6 mm., and females reach 46.5 mm. In a series of 22 adult males from 6.2 kilometers south of Rayón Mesealapa, Chiapas, México, the snout-vent length is 36.9 to 41.6 (mean, 38.9) mm.; the ratio of tibia length to snout-vent length is 0.468 to 0.529 (mean, 0.499); the ratio of foot length to snout-vent length is 0.412 to 0.462 (mean, 0.438); the ratio of head length to snout-vent length is 0.286 to 0.369 (mean, 0.332); the ratio of head width to snout-vent length is 0.331 to 0.395 (mean, 0.355), and the ratio of the diameter of the tympanum to that of the eye is 0.365 to 0.510 (mean, 0.440). These specimens are from the known western extremity of the range, but three individuals having snout-vent lengths of 39, 40, and 40 mm. from Finca San Francisco, El Quiché, Guatemala (the known eastern extremity of the range), are encompassed within the variation exhibited by the specimens from the area of Rayón Mesealapa.

The head is nearly as broad as the body, and the top of the head is flat. In dorsal profile, the snout is basically truncate at the level of nostrils but sharply pointed terminally; in lateral profile, the snout is truncate. The snout is short; its length is no longer than the length of the orbit. The nostrils are protuberant, directed dorsolaterally, and situated near the tip of the snout. The canthus is elevated and sharply rounded; the loreal region is flat, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct in most specimens, but in some the tympanic ring is obscured posteriorly. The tympanum is posterior to the ventral border of the eye and is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are short and moderately robust; in breeding males they are hypertrophied. A row of low tubercles is present on the ventrolateral edge of the forearm and a weak transverse dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs; the width of the disc on the third fingers is greater than the diameter of the tympanum. The subarticular tubercles are large and subconical; in some individuals, the distal tubercle on the fourth finger is bifid. The supernumerary tubercles are small and conical; they are irregularly arranged in a single row on the proximal segments of the first and fourth fingers and in one or two rows on the proximal segments of the second finger, and usually in two rows on the proximal segment of the third finger. A flattened, bifid palmar tubercle is present. The prepollex is enlarged and curved distally; in some males the sharp prepollical spine protrudes from the distal end of the prepollex. 269B). The legs are moderately short and stout; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the posterior corner of the eye. A few small tubercles are present on the heel, and in some specimens, a faint transverse dermal fold is present on the heel. A distinct, flap-like tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, elliptical, and elevated; no distinct outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately large and subconical. The supernumerary tubercles are large, subconical, and arranged in a single row on the proximal segment of each digit. The supernumerary tubercles are also present on the more distal segments of the third and fourth toes. The toes are about three-fourths webbed (fig. 270B). The webbing extends from the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short, narrow anal sheath is present. A pair of large tubercles is present below the anal opening. The skin on the dorsum is smooth or has a few small scattered tubercles. The skin on the throat, belly, and ventral surfaces of the thighs is strongly granular, whereas that on the other ventral surfaces is smooth. The tongue is ovoid or cordiform; in most individuals a shallow notch is present both anteriorly and posteriorly, but in some specimens there is no anterior notch. The tongue is barely free behind. The denticulous processes of the prevomers are short, transverse elevations between the posterior margins of the small, ovoid choanae. There are three to five teeth on each elevation. The number of maxillary and premaxillary teeth (one side only) varies from 41 to 58. The vocal slits extend from the midlateral base of the tongue to the angles of the jaw. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Plectrohyla ixil* consists of a brown or olive-tan dorsum with a yellowish orange lateral stripe, bordered below by a dark brown line (pl. 68, fig. 2). The dorsum varies from olive-brown to tan or dull greenish gray. In some individuals, there are scattered brown flecks or small spots on the dorsum; there are no distinctive transverse marks on the limbs. The side of the head is darker brown. A dark brown line extends from the nostril to the eye and thence along the supratympanic fold to a point above the insertion of the arm and then posteroventrally on the flanks towards the groin. A pale creamy yellow or yellowish orange stripe begins just posterior to the eye and extends to the groin. A dark brown or black vertical bar usually is present below the eye. The anterior and posterior surfaces of the thighs are gray or dark grayish brown, and the venter is pale gray. The vocal sac is dark gray. The iris is deep bronze reticulated with black.

In preservative, the dorsum is dull gray or brown with or without darker markings. The pale lateral stripe is tan or creamy gray, and the venter is gray.

**TADPOLES:** Six tadpoles in developmental stage 25 from a stream 6.2 kilometers south

of Rayón Mesealapa, Chiapas, México, have body lengths of 11.5 to 13.8 (mean, 12.6) mm. and total lengths of 32.4 to 40.7 (mean, 36.1) mm. Three tadpoles in developmental stage 37 from the same locality have body lengths of 15.5 to 16.5 (mean, 16.0) mm. and total lengths of 43.5 to 47.3 (mean, 45.9) mm. In a typical tadpole in developmental stage 37 the body is ovoid in dorsal view; the dorsal profile of the snout is rounded; and in lateral profile the snout slopes gradually to its anterior terminus. The eyes are small and directed dorsolaterally. The nostrils are situated about midway between the eyes and the tip of the snout and are directed anterolaterally. The opening of the sinistral spiracle is directed posterodorsally at a point about on the midline slightly posterior to the midlength of the body. The anal tube is long and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The caudal fins are low; at midlength of the tail the depth of the caudal musculature is half again the depth of either the dorsal or ventral fins. The dorsal fin does not extend onto the body (fig. 275B).

The body is dark brown dorsally and dull gray ventrally. The caudal musculature is pale brown with dark brown blotches, flecks, and reticulations. In preservative, the dorsum is dull brown and the venter is gray. The caudal musculature is pinkish tan, and the caudal fins are translucent. The tail is marked by reddish brown blotches and flecks.

The mouth is ventral and large; its width is equal to about two-thirds of the greatest width of the body. There is no lateral fold and the mouth is completely bordered by a single row of small papillae. Medial to this fringing row are scattered larger papillae, especially laterally. The beaks are slender. The upper beak is broad and only slightly curved laterally; it bears pointed serrations, three or four of which, on either side are noticeably enlarged. The lower beak is broadly arched and bears fine serrations. There are two upper and three lower rows of teeth. The upper rows are long and subequal in length; in most specimens, the second upper row is narrowly interrupted medially. The first and second lower rows are equal in length, but noticeably shorter than



the upper rows, whereas the third lower row is somewhat shorter than the other lower rows. In some specimens, the first lower row is narrowly interrupted medially (fig. 276B).

Stuart (1942, p. 9) described and illustrated this tadpole under the name of "Form y."

**MATING CALL:** The call of *Plectrohyla ixil* consists of a single note repeated at short intervals. One recording provides the following data. The note repetition rate is seven notes per minute and the duration of notes varies from 0.18 to 0.26 of a second. There are approximately 200 pulses per second; the fundamental frequency in this poorly modulated note is at about 700 cycles per second, and the dominant frequency is at about 2100 cycles per second (pl. 35, fig. 3).

**NATURAL HISTORY:** *Plectrohyla ixil* inhabits cloud forests on the Atlantic slopes of the highlands of Chiapas and Guatemala. My observations on this species have been made on the Atlantic slopes in Chiapas along streams at elevations between 1550 and 1690 meters, above the village of Rayón Mescalapa. Males have been observed calling in February, June, and August. Adults have been found on rocks in the streams, both at night and by day. Calling males were observed only on the stems of vegetation overhanging the stream at night. I found one adult in the axil of an elephant ear plant by day, and Smith and Brandon (1968, p. 53) reported two individuals in axils of those plants. Metamorphosing young were obtained in June and August. Seven young having tail-stubs of 3 to 20 mm. had snout-vent lengths of 17.4 to 20.0 (mean, 18.8) mm. A fully transformed juvenile has a snout-vent length of 25.2 mm.

Stuart (1942) obtained this species at Finca San Francisco, Departamento El Quiché, Guatemala, on July 31, 1940. At that time, he obtained two juveniles having tail-stubs of about 10 mm. The juveniles have snout-vent lengths of approximately 15.5 mm.

**REMARKS:** The general structure of this species indicates a relationship with *Plectrohyla matudai*. Furthermore, the presence of enlarged serrations on the upper beak in the tadpoles seems to ally *ixil* and *matudai*. In light of their allopatric distribution, it is conceivable that they are subspecifically related.

However, differences in coloration, tuberosity, and mouthparts of the tadpoles are of sufficient magnitude and constancy within each species that it seems better to recognize them as distinct species until evidence of intergradation is found.

Smith and Brandon (1968, p. 53) discussed specimens of this species from 25 kilometers south of Ixhuitán, Chiapas, México, under the name of *Plectrohyla matudai*; it is evident from their description of the tadpoles that they had specimens of *Plectrohyla ixil*.

**ETYMOLOGY:** The specific name refers to the Ixil Indians, a subgroup of the Mame ethnic group, in northern El Quiché, Guatemala. The "x" is pronounced like "sh"; hence, "ē-shel'."

**DISTRIBUTION:** *Plectrohyla ixil* occurs at elevations of 1100 to 1700 meters on the Atlantic slopes of the highlands of Chiapas, México, and western Guatemala (fig. 277).

See Appendix 1 for the locality records of the 99 specimens examined.

### *Plectrohyla sagorum* Hartweg

*Plectrohyla sagorum* Hartweg, 1941, p. 2 [holotype, U.M.M.Z. No. 88862 from Cerro Ovando, Distrito Soconusco, Chiapas, México, elevation 1800 meters; Norman Hartweg collector]. Smith and Taylor, 1948, p. 73. Stuart, 1963, p. 40.

**DIAGNOSIS:** This moderately small species (51 mm. in snout-vent length) has vocal slits, a long, pointed prepollical spine, a smooth or weakly tuberculate dorsum, and an acuminate snout with a vertical rostral keel. This combination of characters readily separates *sagorum* from all other species in the genus, except *quicchi*, the only other species with a vertical rostral keel. In *quicchi*, the snout is blunt, and the dorsum is strongly tubercular; furthermore, in *quicchi* the flanks are marked with large brown spots, whereas the flanks are marked with small dark flecks in *sagorum*. The other species having vocal slits (*ixil* and *matudai*) lack a vertical rostral keel. The remaining members of the genus are larger (except *lacertosa*) and lack vocal slits.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 45.5 mm., and females reach 51.9 mm. In a series of 15 males from Volcán Tacaná, Chiapas, México, and Granja Lorena, Departamento Quet-

zaltenango, Guatemala, the snout-vent length is 33.6 to 45.5 (mean, 39.3) mm.; the ratio of tibia length to snout-vent length is 0.462 to 0.591 (mean, 0.520); the ratio of foot length to snout-vent length is 0.392 to 0.484 (mean, 0.438); the ratio of head width to snout-vent length is 0.285 to 0.346 (mean, 0.315); the ratio of head length to snout-vent length is 0.308 to 0.385 (mean, 0.350), and the ratio of the diameter of the tympanum to that of the eye is 0.333 to 0.719 (mean, 0.496). Four females from the same area have snout-vent lengths of 39.6 to 51.9 (mean, 44.6) mm.

The head is as wide as, or slightly broader than the body. The top of the head is flat. In dorsal profile, the snout is pointed; a narrow, vertical rostral keel is present. In lateral profile, the snout is truncate. The snout is moderately short; the nostrils are barely protuberant and are situated about two-thirds of the distance from the eyes to the tip of the snout. The snout is elevated and sharply angular; the loreal region is flat, and the lips are thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which in most specimens is otherwise distinct, and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arms are short and robust; they are hypertrophied in some breeding males. Numerous tubercles are present on the ventrolateral edge of the forearm, and a distinct transverse fold is present on the wrist. The fingers are long and slender and bear moderately large discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; in some individuals the distal tubercle on the fourth finger is barely bifid. The supernumerary tubercles are large and subconical; they are arranged in a single row on the proximal segments of each digit, except near the palm, where additional tubercles are present. A large, bifid palmar tubercle is present. The prepollex is moderately enlarged and terminally curved. In some individuals, a prepollical spine protrudes through the termi-

nus of the prepollex. The fingers are webbed only basally (fig. 269C). The legs are moderately short and stout; the heels of the adpressed limbs overlap by about one-sixth of the length of the shank. The tibiotarsal articulation extends to the eye. Numerous small tubercles and a faint transverse dermal fold are present on the heel. An elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately large, flat, ovoid, and visible from above. Numerous small tubercles are present on the tarsus so it is not possible to determine if an outer metatarsal tubercle, as such, is present. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are moderately large and subconical. The toes are about two-thirds webbed (fig. 270C). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short, narrow anal sheath is present. The anal sheath is bordered above by a transverse fold and below by distinct tubercles. The skin on the dorsum bears many small tubercles; that on the chin, belly, and ventral surfaces of the thighs is strongly granular, whereas the skin on the other ventral surfaces is smooth. The tongue is ovoid, longer than wide, shallowly notched anteriorly and posteriorly, and barely free behind. The denticulate processes of the prevomers are small, rounded, widely separated elevations between the moderately large rounded choanae. There are three or four teeth on each elevation. The number of maxillary and premaxillary teeth (one side only) varies from 34 to 45. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is

single, median, subgular, and only moderately distensible.

The general coloration of *Plectrohyla sagorum* is dull brown with small irregular, slightly darker brown spots on the dorsal surfaces (pl. 68, fig. 3). The flanks are tan and are marked by fine dark brown reticulations or brown flecks. In some individuals, small cream spots are also present on the flanks. The posterior surfaces of the thighs are dull dark brown, and the belly is gray. The vocal sac is dark grayish brown. The iris is deep bronze with fine black reticulations.

In preservative, the dorsum varies from grayish brown to dull brown with faint or distinct dark brown flecks on the body and limbs. The flanks usually are somewhat paler and marked by numerous brown flecks or small spots. The venter is dull creamy tan or pale gray.

**TADPOLES:** A typical tadpole in developmental stage 32 has a body length of 13.2 mm. and a total length of 36.9 mm. The body is ovoid, no wider than deep. In dorsal and lateral profiles, the snout is rounded. The eyes are small and directed dorsolaterally. The nostrils are directed anterolaterally at a point slightly closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is on the midline slightly posterior to the midlength of the body. The anal tube is moderately long and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The fins are narrow; at midlength of the tail, the depth of the caudal musculature is greater than the depth of either the ventral or dorsal fins; the dorsal fin is shallower than the ventral one and does not extend onto the body (fig. 275C).

The body is dark gray brown with some faint darker mottling. The caudal musculature is paler brown and the fins are transparent. The tail is heavily spotted with dark gray. In preservative, the body and caudal musculature is dark brown with darker brown flecks and spots on the caudal musculature and fins.

The mouth is ventral; its width is equal to about two-thirds of the greatest width of the body. The mouth lacks lateral folds and is completely bordered by a single row of

small papillae. A row of larger papillae is present medial to the fringing row; a few small papillae are present lateral to the beaks. The beaks are well developed and bear long, pointed serrations of equal length. The upper beak is in the form of a broad arch with moderately robust lateral processes; the ventral beak is massive and V-shaped. There are two upper and three lower rows of teeth. The upper rows are long and equal in length, and the second upper row is narrowly interrupted medially. The lower rows are somewhat shorter than the upper ones, equal in length, and complete (fig. 276C).

This is the tadpole described by Hartweg and Orton (1941, p. 5) as "Form b."

**MATING CALL:** Recordings of the call of *Plectrohyla sagorum* are not available. Taylor and Smith (1945, p. 598) described the call of this species as a "slightly drawn out, coarsely trilled, nasal quaaaek."

**NATURAL HISTORY:** *Plectrohyla sagorum* inhabits cloud forest, where it breeds at night in cascading mountain streams and spends the days in bromeliads. Taylor and Smith (1945, p. 597) noted that in April, 1940, both adults and juveniles were found in bromeliads on Cerro Ovando, and that males were calling from bromeliads by day. At Granja Lorena, Guatemala, on July 21, 1966, males were calling from low branches of bushes along a small stream at night. Tadpoles were found in gravel-bottomed pools in the streams. Tadpoles were found in similar habitats at 10.4 kilometers west-southwest of San Martín Sacatepequez, Guatemala, on July 30, 1960 and on February 19, 1961. Adults were found in bromeliads on Volcán Tacaná, Chiapas, on August 18, 1965. These observations indicate that calling apparently takes place throughout the year and probably breeding also takes place throughout the year. Furthermore, this species, perhaps more than any other *Plectrohyla*, utilizes bromeliads as daytime retreats.

**REMARKS:** *Plectrohyla sagorum* is known to occur sympatrically with at least four other members of the genus (*avia*, *matudai*, *guatemalensis*, and *hartwegi*). Of these, the species seems to be ecologically most like *matudai*, which also inhabits small streams. The other species tend to inhabit the larger



streams, although at Granja Lorena, Guatemala, both *avia* and *guatemalensis* were found along the same small stream with *sagorum*.

**ETYMOLOGY:** The specific name is derived from the Latin *saga* meaning soothsayer; Hartweg (1941, p. 2) proposed the name "in memory of the few witchcraft-practicing Indians who inhabit that eerie mountain [Cerro Ovando, Chiapas]."

**DISTRIBUTION:** *Plectrohyla sagorum* occurs at elevations of 1500 to 2050 meters on the Pacific slopes of the Sierra Madre from south-central Chiapas, México, southeastward to north-central El Salvador (fig. 278).

See Appendix 1 for the locality records of the 94 specimens examined.

### *Plectrohyla quecchi* Stuart

*Plectrohyla quecchi* Stuart, 1942, p. 1 [holotype, U.M.M.Z. No. 89086 from Barranca Las Palmas, 2

kilometers north of Finca Los Alpes (43 kilometers east and slightly south of Cobán, Alta Verapaz, Guatemala, elevation 1015 meters; Laurence C. Stuart collector]; 1963, p. 40.

**DIAGNOSIS:** This small species (47 mm. in snout-vent length) has vocal slits, a long, pointed prepollical spine, a tuberculate dorsum, and a blunt snout with a vertical rostral keel. This combination of characters readily separates *quecchi* from all other species in the genus, except *sagorum*, which also has a vertical rostral keel. The latter species has an acuminate snout and a smooth or weakly tuberculate dorsum. In *quecchi*, large brown spots are present on the flanks, whereas in *sagorum* the flanks are marked with small dark flecks. The other species having vocal slits (*ixil* and *matudai*) lack a vertical rostral keel. The remaining members of the genus are larger and lack vocal slits.

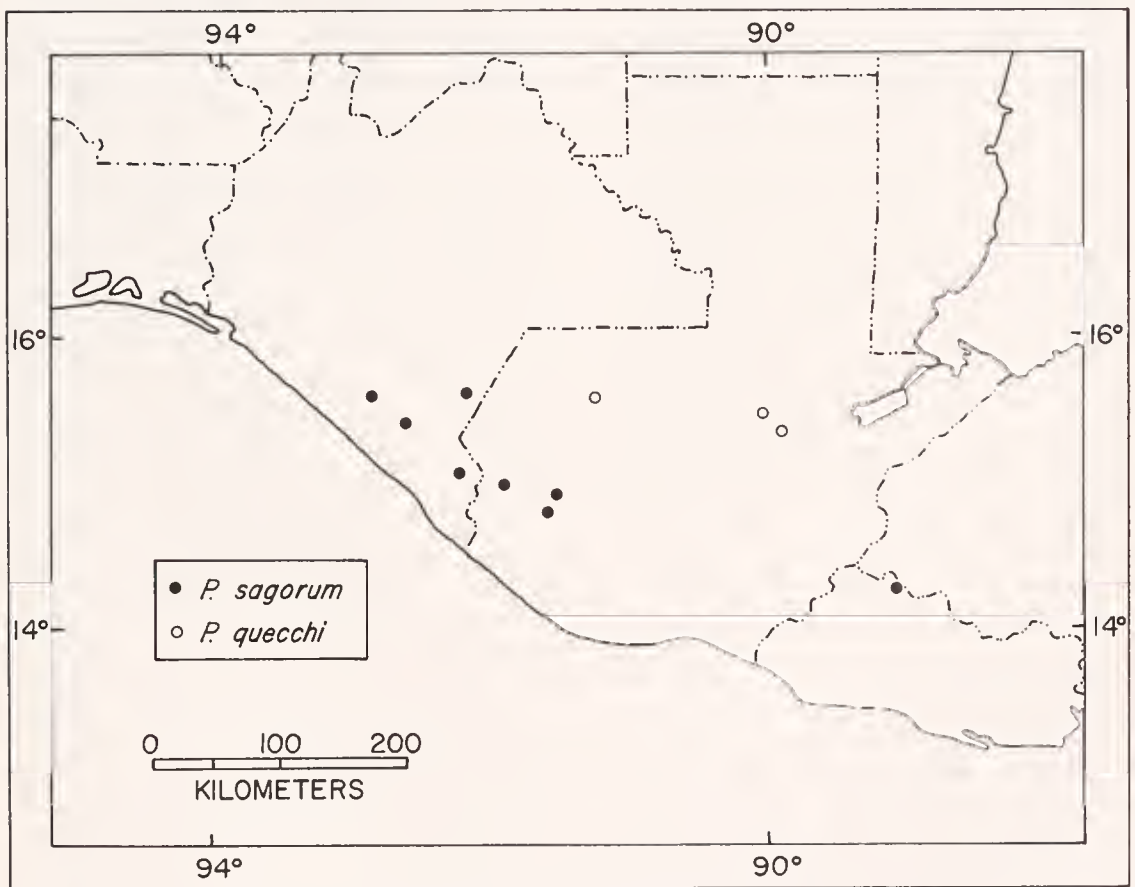


FIG. 278. Distribution of *Plectrohyla sagorum* and *Plectrohyla quecchi*.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 44.0 mm., and females reach 46.7 mm. In a series of eight adult males, from Finca Los Alpes, Departamento Alta Verapaz, Guatemala, the snout-vent length is 40.4 to 43.8 (mean, 42.2) mm.; the ratio of tibia length to snout-vent length is 0.514 to 0.554 (mean, 0.531); the ratio of foot length to snout-vent length is 0.460 to 0.493 (mean, 0.480); the ratio of head length to snout-vent length is 0.294 to 0.338 (mean, 0.318); the ratio of head width to snout-vent length is 0.342 to 0.390 (mean, 0.368), and the ratio of the diameter of the tympanum to that of the eye is 0.346 to 0.463 (mean, 0.411). The single known female from the same locality has a snout-vent length of 46.7 mm. and does not differ from the males in proportions.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is truncate. A narrow, vertical rostral keel is evident on the dorsal part of the snout. The snout is short; its length is slightly less than the diameter of the eye. The nostrils are nearly terminal and are directed dorsolaterally. The canthus is elevated and slightly angular. The loreal region is barely concave and the lips are thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which in some specimens is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum, whereas in other specimens, the tympanum is barely evident.

The arms are short and robust, especially in breeding males. A row of small tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs; the width of the disc on the third finger is greater than the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; none is noticeably bifid. The supernumerary tubercles are moderately large and subconical; they are present on the proximal segments of each digit and arranged

in a single row on the distal part of the segments, but in some individuals irregularly arranged proximally. The flat, bifid palmar tubercle is present. The prepollex is moderately enlarged and distally curved; in some males the tip of the prepollical spine protrudes through the distal end of the prepollex. The webbing on the hands is vestigial (fig. 269D). The hind limbs are moderately short and stout; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the eye. A few small tubercles and a distinct transverse dermal fold is present on the heel. A distinct tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is long, elliptical, flat, and visible from above. A small conical outer metatarsal tubercle is present. The toes are long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are large and conical; they are arranged in a single row on the proximal segments of each digit. The toes are about two-thirds webbed (fig. 270D). The webbing extends from the middle of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally near the midlevel of the thighs. A short, narrow anal sheath is present. A transverse dermal fold exists above the anal sheath, and vertical dermal folds are present below the anal opening. The skin on the dorsum is tuberculate and that on the throat, belly, and ventral surfaces of the thighs is strongly granular, whereas the skin on the other ventral surfaces is smooth. The tongue is ovoid, longer than wide, shallowly notched anteriorly and posteriorly, and barely free behind. The denticulous processes of the prevomers are small, elliptical, widely separated elevations between the moderately large ovoid,

choanae. Each elevation bears three or four teeth. The number of premaxillary and maxillary teeth varies from 47 to 53. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular and moderately distensible.

The general coloration of *Plectrohyla quecchi* is pale tan, olive-tan, or pale grayish brown above with dark brown spots on the somewhat paler flanks (pl. 68, fig. 4). A few faint darker spots are present on the dorsum. The posterior surfaces of the thighs are tan or pale brown. The belly is grayish with gray or brown suffusion or mottling and the vocal sac is dull olive-green with cream spots. The iris is deep bronze with fine black reticulations.

In preservative, the dorsum varies from dull grayish tan to dark brown with or without faint darker flecks or reticulations. The flanks are marked by bold brown spots, and the venter is mottled with gray or brown, especially on the chest.

**TADPOLES:** A typical tadpole in developmental stage 34 has a body length of 15.0 mm. and a total length of 42.0 mm. The body is ovoid, no wider than deep. The snout is bluntly rounded in dorsal and lateral profiles. The eyes are moderately small and directed dorsolaterally; the nostrils are situated about midway between the eyes and the tip of the snout and are directed anterolaterally. The opening of the sinistral spiracle is about on the midline about midlength of the body. The cloacal tube is long and dextral. The caudal musculature is heavy and extends nearly to the tip of the rounded tail. The fins are shallow, and the dorsal fin does not extend onto the body. At midlength of the tail, the caudal musculature is deeper than either the dorsal or ventral fins, which are of approximately equal depth throughout their length (fig. 275D).

In preservative, the body is pale brown; the caudal musculature is tan, and the caudal fins are transparent. Large dark brown blotches are present on the tail.

The mouth is ventral; its width is equal to about two-thirds of the greatest width of the body. There is no lateral fold. The

mouth is completely bordered by a single row of small papillae; numerous larger papillae are present medially to the fringing papillae. The beaks are well developed and possess long, pointed serrations of equal length. The upper beak is in the form of a broad arch and lacks noticeable lateral processes; the lower beak is moderately robust and broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are long and equal in length, and the second upper row is narrowly interrupted medially. The lower rows are shorter than the upper ones; the first and second lower rows are equal in length, whereas the third is shorter (fig. 276D).

This is the tadpole described as "Form z" by Stuart (1942, p. 10).

**MATING CALL:** Recordings of the call of this species are not available, Stuart (1942, p. 4) stated that the call is a "harsh quack repeated at rather long intervals."

**NATURAL HISTORY:** *Plectrohyla quecchi* is an inhabitant of cloud forest. The only observation of adults was made at Finca Los Alpes, Departamento Alta Verapaz, Guatemala. There in February, 1940, Stuart found the adults between boulders and pebbles in the water in a mountain stream. I obtained adults there at night in July, 1961. The frogs were found on bushes and vines overhanging a stream at night, but one male was obtained from a vine by day.

The tadpoles have been taken from gravel-bottomed pools in streams.

**REMARKS:** This species obviously is closely related to *P. sagorum*, from which it differs principally in the shape of the snout and in the amount of dark pigmentation on the flanks. The two species seem to represent vicarious populations of a formerly more widespread stock.

**ETYMOLOGY:** The specific name refers to the Quecchi Indians of Alta Verapaz, Guatemala. The name is pronounced "kek-ehi'."

**DISTRIBUTION:** *Plectrohyla quecchi* is known from elevations of 1000 to 1600 meters on the slopes of the Atlantic highlands in central Guatemala (fig. 278).

See Appendix 1 for the locality records for the 22 specimens examined.



***Plectrohyla glandulosa* (Boulenger)**

*Hyla glandulosa* Boulenger, 1883, p. 164 [syntypes, B.M.N.H. Nos. 1947.2.20.40 and 41 from "Guatemala"; presented by Frederick D. Godman]. Günther, 1901 (1885-1902), p. 281. Duellman, 1964c, p. 455 [synonymized *Plectrohyla cotzieensis* Stuart, 1948a, with *Hyla glandulosa* Boulenger, 1883].

*Plectrohyla cotzieensis* Stuart, 1948a, p. 17 [holotype, U.M.M.Z. No. 95902 from the source of the Río Cuilco, on the slopes of Cerro Cotzic, 2 kilometers northwest of Ixchiguán, Departamento San Marcos, Guatemala; Laurence C. Stuart collector]. Stuart, 1963, p. 39.

**DIAGNOSIS:** This moderate-sized species (50 mm. snout-vent length) has a smooth or weakly tuberculate dorsum. The prepollical process is short, flat, and blunt, and the dorsum is mottled gray and dull green. Males lack vocal slits. Of the other species lacking vocal slits, *guatemalensis* and *hartwegi* each differs by having a bifid prepollical spine and a tuberculate dorsum; *avia* has a long, pointed prepollical spine and a short, blunt snout, whereas *pynochila* has a short, flat, and blunt prepollical spine like that in *glandulosa* but differs by having a tuberculate dorsum and a round snout. *Plectrohyla lacertosa* has an elongate, round, terminally blunt prepollical spine, a short snout, and a brown dorsum. Other species of *Plectrohyla* have vocal slits in males and eurved, terminally pointed prepollical spines.

**DESCRIPTION:** Males of this moderately large species attain a snout-vent length of 49.1 mm., and females reach 49.7 mm. In a series of 12 males from 8 kilometers south of Paquix, Departamento Huehuetenango, Guatemala, the snout-vent length is 42.2 to 49.1 (mean, 44.6) mm.; the ratio of tibia length to snout-vent length is 0.471 to 0.543 (mean, 0.513); the ratio of foot length to snout-vent length is 0.462 to 0.524 (mean, 0.480); the ratio of head length to snout-vent length is 0.274 to 0.321 (mean, 0.296); the ratio of head width to snout-vent length is 0.323 to 0.384 (mean, 0.352), and the ratio of the diameter of the tympanum to that of the eye is 0.255 to 0.537 (mean, 0.378). Five females from the same locality have snout-vent lengths of 39.3 to 49.7 (mean, 44.3) mm. They do not differ significantly from the males in proportions except that the ratio of the diameter of the tympanum to that of the eye is 0.356 to 0.558 (mean, 0.431).

The head is slightly narrower than the body, and the top of the head is flat. The snout in dorsal profile is acuminate; in lateral profile it is truncate. The snout is short, its length is about equal to the diameter of the eye. The nostrils are barely protuberant and are situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is barely elevated and moderately angular. In breeding males, the loreal region is flat, and the lips are thick and swollen. In females, and subadult males, the loreal region is slightly concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is barely evident and is separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long, slender in females, and robust in males. A row of low tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear large discs; the width of the disc on the third finger is noticeably greater than the diameter of the tympanum. The subarticular tubercles are moderately large, round, and flattened; none is bifid. The supernumerary tubercles are small and subconical; they are arranged in a single row on the proximal segments of each digit. A small, diffuse palmar tubercle is present. The prepollex is enlarged and quadrangular. The webbing on the hands is vestigial (fig. 271C). The legs are moderately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the eye. A few small tubercles and a transverse dermal fold are present on the heel. In all specimens a distinct inner tarsal fold extends the full length of the tarsus. In specimens from the southwestern highlands of Guatemala, there is a distinct outer tarsal fold. In specimens from the highlands of central and southeastern Guatemala, the outer tarsal fold is weak, and in most specimens from the Sierra de los

Cuchumatanes in northwestern Guatemala, the outer tarsal fold is absent or represented by a row of indistinct tubercles. The inner metatarsal tubercle is elliptical and flat. No outer metatarsal tubercle, as such, exists. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are small and round, and the supernumerary tubercles are moderately small and conical. The toes are about two-thirds webbed (fig. 272A). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the penultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth, and from the middle of the antepenultimate phalanx of the fourth to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short anal sheath is present, but a distinct transverse anal flap and anal tubercles are present. The skin on the dorsum is weakly or moderately tubercular; that on the flanks is smooth or possesses a few small scattered tubercles. The skin on the throat, belly, and ventral surfaces of the thighs is granular, and that on the ventral surfaces of the shanks is smooth. The tongue is nearly round, shallowly notched anteriorly and posteriorly, and barely free behind. The dentigerous processes of the prevomers are small, widely separated, transverse ridges between the posterior margins of the moderately small, ovoid choanae. There are one to three long, pointed teeth on each ridge. The number of maxillary and premaxillary teeth (one side only) varies from 23 to 30. Vocal slits and a vocal sac are absent.

The general coloration of adult males is usually green or dull olive-green above with irregular olive-brown or dark brown markings (pl. 69, fig. 1). Some individuals are dull olive-brown or grayish brown above with faint darker brown markings. The posterior surfaces of the thighs and webbing of the feet are gray, and the venter is grayish white. Adult females usually are nearly uniform

green above (pl. 69, fig. 2). In many individuals, a distinct brown or tan stripe is present on the eanthus and supratympanic fold. The flanks are creamy tan or pinkish tan, and the venter is creamy white. The posterior surfaces of the thighs and the webbing is pale tan. There is a creamy white line on the outer edge of the tarsus and a transverse white line above the anal opening. In both sexes, the iris is bronze flecked with black.

The intensity of the dorsal pigmentation is subject to change. Some females change to dark olive-brown or gray, whereas some males that were rather pale green with olive-brown markings change to dark olive-brown with dark brown markings. Juveniles are pale green above and have a white line on the tarsus and above the anus. The throat and belly are white and the ventral surfaces of the limbs and the webbing are yellow.

In preservative, the dorsum is dull grayish tan or dull brown with darker grayish brown markings. The posterior surfaces of the thighs are grayish tan, and the venter is dirty creamy white.

**TADPOLES:** Large series of tadpoles were obtained from various localities in the Sierra de Los Cuchumatanes in Guatemala. Tadpoles in developmental stage 25 apparently undergo a considerable amount of growth. In a series of 31 specimens in that developmental stage the body length varies from 8.6 to 13.0 (mean, 11.1) mm., and the total length varies from 20.5 to 31.5 (mean, 26.5) mm. The largest tadpole examined was in developmental stage 37 and had a body length of 21.7 mm. and a total length of 56.8 mm.

A typical tadpole in developmental stage 28 has a body length of 17.5 mm., and a total length of 45.0 mm. The body is rather elongate and bluntly rounded anteriorly and posteriorly. The body is as wide as deep. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is somewhat more sharply rounded. The eyes are widely separated, small, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is about on the midline at approximately midlength of the body. The anal tube is moderately long and dextral. The caudal

musculature is robust and extends nearly to the tip of the rounded tail. At midlength of the tail the depth of the caudal musculature is slightly more than the depth of either the dorsal or ventral fins. The dorsal fin does not extend onto the body (fig. 275E).

The body is brown with greenish gold lichenous markings laterally and ventrally. The tail is tan with dark brown flecks and blotches. The iris is pale bronze. In preservative, the body is dark grayish brown, and the caudal musculature is creamy tan. The caudal fins are translucent, and the entire tail is marked with dark brown flecks or small blotches.

The mouth is ventral and moderately large; its width is equal to about three-fifths of the greatest width of the body. The mouth lacks a lateral fold, but is completely bordered by one row of small papillae. Medial to the fringing row is a row of larger papillae on the anterior and posterior lip. There are no papillae lateral to the beak. The upper beak is moderately slender, lacks lateral processes, and bears short, pointed serrations that are of approximate equal length. The lower beak is massive, broadly V-shaped, and bears short pointed serrations. There are two upper and three lower rows of teeth. The upper rows are long and about equal in length; the second upper row is narrowly interrupted medially. The lower rows are complete; the first and second lower rows are equal in length but shorter than the other rows, and the third lower row is noticeably shorter than the others (fig. 276E).

The characteristics of these tadpoles agree with those described for this species by Stuart (1951, p. 51). As noted by Stuart, small specimens (those less than 10 mm. in developmental stage 25) do not have the mouthparts fully developed. The keratinization of the beaks is incomplete, and the formation of the rows of teeth is incomplete. Apparently, the third lower row is the last to develop.

**MATING CALL:** The absence of vocal slits and a vocal sac preclude the presence of a voice in this species.

**NATURAL HISTORY:** *Plectrohyla glandulosa* inhabits the pine-cypress forest, fir forest, and montane meadows at high elevations in Guatemala. Adults are usually found along small

rivulets. Stuart (1948a, p. 18) reported finding adults "beneath rocks and clumps of sod in shallow tricklets emerging from springs in the flanks of Cerro Cotzic" [2 kilometers northwest of Ixchiguan, San Marcos, Guatemala]. In July, 1960, and in March, 1966, I found adults sitting on rocks under banks and small cascades in a small stream in a montane meadow 8 kilometers south of Paquix in the Sierra de Los Cuchumatanes, Guatemala. A few individuals were observed sunning on rocks or on bunch grass in and along the stream.

The tadpoles usually are found in quiet pools in streams or adhering to the lee-side of rocks in the streams. Stuart (1951, p. 52) stated: "Both tadpoles and adults have been taken in tiny rivulets in the pine-cypress zone and in quiet spring-fed pools, where this species is associated with *Bufo bocourti*. Thus, though apparently adapted to life in the swift mountain stream, the species can and does invade the lenitic environment." I obtained both tadpoles and metamorphosing young from the shallow Laguna de Vejcha at an elevation of 3040 meters in the Sierra de Los Cuchumatanes. At that locality the tadpoles were in shallow water having a temperature of 16.5 degrees centigrade.

Stuart (1951, p. 51) stated: "This species apparently has an extended breeding season, a condition which seems to obtain in most of the stream salientians of Guatemala. Females with eggs apparently ready for deposition were secured at Ixchiguan on April 23, and one in same condition was taken on Maria Tucum on August 4. Tadpoles as small as 6 mm. and at the transformation stage were secured during early and mid-April at Ixchiguan, while transformed juveniles were taken on Maria Tucum on August 4." My observations corroborate those of Stuart; tadpoles in various stages of development and metamorphosing young were obtained in the Sierra de Los Cuchumatanes in July, 1960, and in March, 1966. The tadpoles of *Plectrohyla glandulosa* develop in extremely cold water; consequently, it is highly probable that the duration of the tadpole stage is lengthy and possibly requires more than one year.

At lower elevations, such as at Soledad



Grande, Departamento Japala, Guatemala (elevation 2500 meters), this species has been found in bromeliads. Stuart (1954c, p. 48) reported finding 10 juveniles and one adult female with eggs in bromeliads.

The habits of the frogs of sitting on rocks or clumps of bunch grass in the sun is unique among Middle American hylids. A well-developed melanin layer in the skin apparently protects the animal against the effects of solar radiation.

REMARKS: This species is best known under the name of *Plectrohyla cotzicensis* Stuart, 1948a. Duellman (1964c, p. 455) resurrected Boulenger's *Hyla glandulosa* for this species.

ETYMOLOGY: The specific name is Latin, meaning glandular, and refers to the thick glandular condition of the skin.

DISTRIBUTION: *Plectrohyla glandulosa* oc-

curs at elevations from 2400 to 3500 meters in the highlands of Guatemala and adjacent El Salvador (fig. 279).

See Appendix 1 for the locality records of the 192 specimens examined.

### *Plectrohyla pycnochila* Rabb

*Plectrohyla pycnochila* Rabb, 1959, p. 45 [holotype, A.M.N.H. No. 62667 from "Coyame, Veracruz, México"; Byron Harrell collector].

DIAGNOSIS: This moderate-sized species (60 mm. in snout-vent length) has a tuberculate dorsum and lacks vocal slits. The snout is blunt, and the prepollical process is short, flat, and blunt. The only other species having a short, flat, blunt prepollical process is *glandulosa*, which has a smooth dorsum and an acuminate snout. *Plectrohyla lacertosa* has an elongate, round, terminally blunt prepolli-

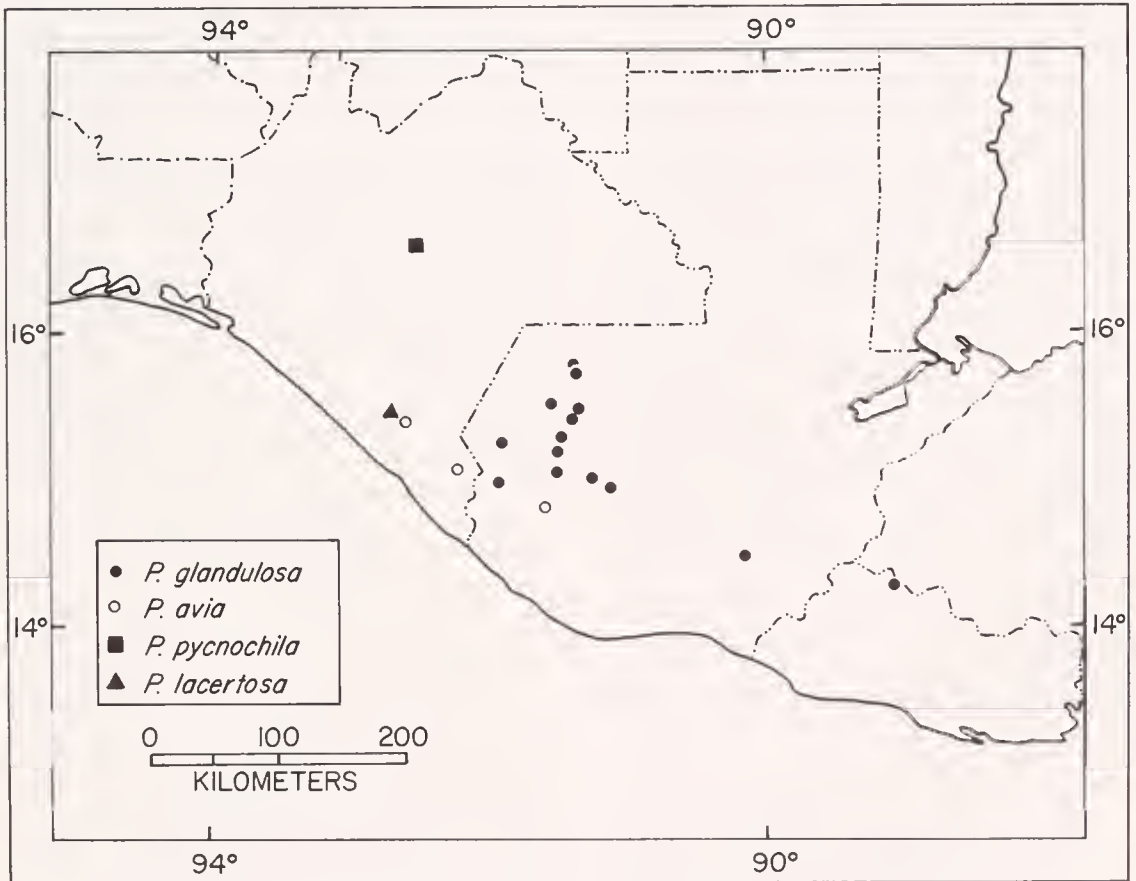


FIG. 279. Distribution of *Plectrohyla lacertosa*, *P. glandulosa*, *P. pycnochila*, and *P. avia*.

cal spine and an acuminate snout. The other members of the genus that lack vocal slits have bifid prepollical spines (*guatemalensis* and *hartwegi*) or a long, pointed prepollical spine (*avia*). The remaining four species (*ixil*, *matudai*, *quecchi*, and *sagorum*) are smaller (less than 50 mm. in snout-vent length) and have vocal slits and long, pointed prepollical spines.

DESCRIPTION: This species is known from two adult males having snout-vent lengths of 52.5 and 60.5 (mean, 56.5) mm. The ratio of tibia length to snout-vent length is 0.502 to 0.581 (mean, 0.542); the ratio of foot length to snout-vent length is 0.463 to 0.530 (mean, 0.497); the ratio of head length to snout-vent length is 0.288 in both; the ratio of head width to snout-vent length is 0.332 to 0.347 (mean, 0.340), and the ratio of the diameter of the tympanum to that of the eye is 0.464 to 0.484 (mean, 0.474).

The head is slightly broader than the body, and the top of the head is flat. In dorsal profile, the upper part of the snout is truncate, whereas the border of the lips is round; in lateral profile, the snout slopes abruptly from the snout to the lips. The snout is short; the nostrils are slightly protuberant and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is slightly elevated and angular; the loreal region is barely concave, and the lips are thick and barely flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arms are moderately long and robust. A row of low tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; none is bifid. The supernumerary tubercles are small and conical; they are present in a single row on the proximal segments of each digit ex-

cept basally on the third and fourth digits where there are additional tubercles. The palmar tubercle is elevated and bifid. The prepollex is rectangular. The fingers are about one-half webbed (fig. 271A). The webbing is vestigial between the first and second fingers and connects the second finger from the base of the penultimate phalanx to the middle of the antepenultimate phalanx of the third and on to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A distinct transverse dermal fold is present on the heel, and a low tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately small and elevated. A minute, conical outer metatarsal tubercle is present. The toes are long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are small, subconical, and arranged in a single row on each digit. The toes are about three-fourths webbed (fig. 272C). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally at the midlevel of the thighs. A short anal sheath is present, and a transverse dermal fold is present above the anal sheath. The skin on the dorsal surfaces is tubercular. The tubercles are small and scattered but distinct. The skin on the throat and chest in one individual is smooth and weakly granular in the other; in both specimens, the skin on the belly and ventral surfaces of the thighs is granular, whereas that on the ventral surfaces of the rest of the limbs is smooth. The tongue is nearly round, shallowly notched anteriorly and posteriorly, and barely free behind. The dentigerous processes of the pre-

vomers are narrowly separated, curved elevations between the small round choanae. There are three to five teeth on each process. The number of maxillary and premaxillary teeth (one side only) varies from 31 to 36. There are no vocal slits or a vocal sac.

The coloration in life is unknown. In preservative, the dorsum is dark gray or grayish brown with a few irregular and scattered bluish tan flecks (pl. 5, fig. 1). The ventral surfaces of the forelimbs and throat are creamy white; the other ventral surfaces are bluish gray. The axilla is white.

**TADPOLES:** The tadpoles of this species are unknown.

**MATING CALL:** The absence of vocal slits and a vocal sac precludes the presence of a voice in this species.

**NATURAL HISTORY:** The single specimen of *Plectrohyla pycnochila* having locality data was obtained at 8 kilometers north-northwest of San Cristóbol de las Casas, Chiapas, México. Dr. Dilford G. Carter, the collector, obtained the frog in a cave in pine-oak forest on a slope well above a small stream.

**REMARKS:** Rabb (1959, p. 45), named *Plectrohyla pycnochila* on the basis of a single male supposedly collected near Coyame, Veracruz, México, in July, 1954, by Byron Harrell. Subsequent collecting in the Los Tuxtlas, that volcanic mountain range in which Coyame is located, failed to reveal the presence of *Plectrohyla* there. There are few streams in Los Tuxtlas, and the only hylid tadpole that has been found in these streams are those of *Hyla miotympanum*. Dr. Byron Harrell has informed me that he is not certain that he obtained the type specimen of *pycnochila* in Los Tuxtlas. He intimated that the specimen may have originated in the highlands of central Chiapas.

**ETYMOLOGY:** The specific name is derived from the Greek *pyknos*, meaning thick, and the Greek *cheilos*, meaning lip, and refers to the characteristically thick lips found in breeding males of *Plectrohyla*.

**DISTRIBUTION:** *Plectrohyla pycnochila* occurs in the highlands of central Chiapas, México; the only definite record is from an elevation of 2400 meters (fig. 279).

See Appendix 1 for the locality records of the two specimens examined.

### *Plectrohyla lacertosa* Bumzahem and Smith

*Plectrohyla lacertosa* Bumzahem and Smith, 1954, p. 64 [holotype, U.I.M.N.H. No. 33693 from "Región de Soconusco," Chiapas, México; Eizi Matuda collector].

**DIAGNOSIS:** This moderately small species (47 mm. in snout-vent length) has a smooth dorsum and an elongate, round, terminally blunt prepollical spine; vocal slits are absent. All other species of *Plectrohyla* have a pointed or bifid prepollical spine, except *glandulosa* and *pycnochila*, which have a relatively short, flat, terminally blunt prepollical process. *Plectrohyla lacertosa* differs from *pycnochila* by having a smooth instead of tuberculate dorsum, and from *glandulosa* by being brown instead of mottled gray and green, and by having a completely concealed tympanum instead of a partly covered one.

**DESCRIPTION:** This species is known solely from one adult male having a snout-vent length of 47.8 mm. The ratio of tibia length to snout-vent length is 0.494; the ratio of foot length to snout-vent length is 0.460; the ratio of the head length to snout-vent length is 0.310, and the ratio of head width to snout-vent length is 0.366.

The head is as broad as the body, and the top of the head is flat. In dorsal profile, the tip of the snout is pointed, but the leading edges of the lips are round. In lateral profile, the snout is truncate. The snout is moderately short; the nostrils are not protuberant and are situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is barely evident and rounded; the loreal region is flat and the lips are grotesquely swollen. A thin dermal fold extends posteriorly from the eye to a point above the insertion of the arm. The tympanum is not visible.

The arms are short and greatly hypertrophied. A dermal fold extends along the ventrolateral edge of the forearm and an immensely heavy dermal is present on the wrist. The fingers are moderately long and slender and bear rather small discs. The subarticular tubercles are moderately small and subconical. No supernumerary tubercles are evident. A flat, seemingly tripartite palmar tubercle is present. The prepollex is much elongated into a terminally blunt process, which is cov-



ered by a horny nuptial exereescence. The fingers are webbed only basally (fig. 271B). The hind limbs are moderately short and stout; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the eye. A thin, transverse dermal fold is present on the heel, and a low, rounded tarsal fold extends the full length of the tarsus. The inner metatarsal tuberele is elliptical, barely rounded in profile, and not visible from above. There is no outer metatarsal tuberele. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubereles are small and conical; low, indistinct supernumerary tubereles are present on the proximal segments of each digit. The toes are about two-thirds webbed (fig. 272B). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. A short anal sheath and a transverse dermal fold above the sheath are present. The skin on the dorsum is smooth, except for a few minute tubereles on the head and in the sacral region. The skin on the belly and ventral surfaces of the thighs is strongly granular, whereas the skin on the other ventral surfaces is smooth. The tongue is round, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are widely separated, small transverse elevations between the minute choanae. There are two and three teeth on the elevations. There are 30 teeth on the maxillary and premaxillary on one side and 31 on the other. Vocal slits and a vocal sac are absent.

The color in life is unknown. In preservative, the dorsum is dark brown; the anterior and posterior surfaces of the thighs, the inner surfaces of the shanks, the ventral surfaces of the body and limbs, and the webbing on the feet are dull tan (pl. 4, fig. 3).

**TADPOLES:** The tadpoles of this species are unknown.

**MATING CALL:** The apparent absence of vocal slits and a vocal sac is suggestive that this species has no call.

**NATURAL HISTORY:** Nothing is known of the natural history of this species.

**REMARKS:** Bumzahem and Smith (1954, p. 64) named and described this species on the basis of a single specimen from the "Región de Soconusco, Chiapas, México, collected by Mr. Eizi Matuda between 1944 and 1949." Not only did the authors name a new species on the basis of a specimen lacking precise locality data, they based their description on an extremely poorly preserved specimen. I am unsure as to the status of *Plectrohyla lacertosa*. Possibly it is a very distinctive species in the genus, but on the basis of the single poorly preserved specimen at hand, it is difficult to ascertain the relationships with the other members of the genus. The hideously swollen lips and the enormously hypertrophied arms are suggestive of a possible disease-ridden frog, perhaps suffering from a form of anuran elephantiasis. Mr. David M. Dennis labored arduously to depict the type specimen in the form of a living frog as shown in Plate 4.

**ETYMOLOGY:** The specific name is Latin meaning muscular and refers to the greatly swollen arms.

**DISTRIBUTION:** *Plectrohyla lacertosa* is known only from the Región de Soconusco, Chiapas, México; the species is not known from any definite locality.

See Appendix 1 for the record of the one specimen examined.

### *Plectrohyla avia* Stuart

*Plectrohyla avia* Stuart, 1952, p. 6 [holotype, U.M.M.Z. No. 102280 from Granja Lorena, 10 kilometers airline northwest of Colomba, Departamento Quetzaltenango, Guatemala; Laurence C. Stuart collector]. Stuart, 1963, p. 39.

**DIAGNOSIS:** This large species (90 mm. snout-vent length) has a smooth dorsum, except for small tubereles on the head. Males have a long, single, pointed prepollical spine and lack vocal slits. The dorsum is uniform green. *Plectrohyla avia* can be distinguished by the above characters from other species

lacking vocal slits; of these, *guatemalensis* and *hartwegi* have bifid prepollical spines and tuberculate skin on the dorsum. *Plectrohyla glandulosa* and *pynochila* have blunt prepollical processes; the latter has a tuberculate dorsum, and the former has a smooth dorsum. Additionally, *glandulosa* differs from *avia* by having a pointed snout and mottled dorsum; in *avia*, the snout is blunt, and the dorsum is uniform green. *Plectrohyla lacertosa* is smaller (47 mm. snout-vent length), is brown above, and has an elongate, round, terminally blunt prepollical spine. Species of *Plectrohyla* not mentioned above have vocal slits and are smaller (less than 50 mm. in snout-vent length); none is uniform green above.

**DESCRIPTION:** This is the largest species in the genus. Males attain a maximum known snout-vent length of 90.4 mm.; the females are unknown. Four adult males have snout-vent lengths of 82.5 to 90.4 (mean, 86.2) mm.; the ratio of tibia length to snout-vent length is 0.483 to 0.532 (mean, 0.509); the ratio of foot length to snout-vent length is 0.470 to 0.487 (mean, 0.478); the ratio of head length to snout-vent length is 0.317 to 0.335 (mean, 0.323); the ratio of head width to snout-vent length is 0.354 to 0.356 (mean, 0.355), and the ratio of the diameter of the tympanum to that of the eye is 0.397 to 0.543 (mean, 0.468).

The head is as broad as the body, and the top of the head is flat. In dorsal profile, the snout is rounded; in lateral profile it is bluntly rounded, nearly truncate. The snout is moderately short, and the nostrils are noticeably protuberant and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is a fold-like ridge; the loreal region is noticeably concave, and the lips are thick and swollen. An extremely heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to the point of insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arms are moderately short and extremely robust. No tubercles are present on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately long

and slender and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and subconical; that on the first finger is bifid. The supernumerary tubercles are small, conical, and arranged in a single row on the proximal segments of each digit. A diffuse palmar tubercle is present. The prepollex is enlarged and curved and in breeding males has a horny nuptial excrecence. The fingers are about one-third webbed (fig. 273A). The webbing between the first and second fingers is vestigial; the webbing extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the eye. A thin transverse dermal fold is present on the heel, and a low, inconspicuous tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, elliptical, and elevated. The outer metatarsal tubercle is low and elliptical. The toes are long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately small and conical; the supernumerary tubercles are small, conical, and arranged in a single row on the digits. The toes are about three-fourths webbed (fig. 273D). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short anal sheath and a supra-anal flap are present. The skin on the dorsum is smooth, except that on the top of the head and on the sides of the head small tubercles are present. The

throat, chest and ventral surfaces of the arms and shanks are smooth, whereas the skin on the belly and ventral surfaces of the thighs is granular. The tongue is ovoid, slightly longer than wide, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are narrowly separated, posteromedially inclined ridges between the moderately small, elliptical choanac. There are one to three teeth on each ridge. The number of maxillary and premaxillary teeth (one side only) varies from 27 to 33. Vocal slits and a vocal sac are absent.

The general coloration of *Plectrohyla avia* is uniform green (pl. 69, fig. 4). The moderate dark green of the dorsum is faded on the sides of the head and flanks. The anterior and posterior surfaces of the thighs are greenish gray, and the venter is grayish white. The iris is bronze.

In preservative, the dorsum is dull bluish gray and the venter is creamy white. There is no trace of a pattern.

**TADPOLES:** The tadpoles of this species are unknown.

**MATING CALL:** This species lacks vocal slits and apparently lacks a vocal sac; it is presumed that it lacks a voice.

**NATURAL HISTORY:** Stuart (1952, p. 6) obtained the type specimen in scrubby forest on April 21, 1949. I observed an adult sitting on a branch over a small stream at the type locality in July, 1966. Two specimens were obtained in August along a stream on Volcán Tacaná, Chiapas. Presumably, this species is like others in this genus and breeds in mountain streams.

**REMARKS:** The humerus in this species is modified by having extensively developed ridges, presumably for the attachment of the large brachial muscles (fig. 274).

**ETYMOLOGY:** The specific name is Latin, meaning grandmother, and alludes to the large size of this species.

**DISTRIBUTION:** *Plectrohyla avia* is known from cloud forest at elevations of 1700 to 2000 meters on the Pacific slopes of the Sierra Madre from south-central Chiapas, México, to southwestern Guatemala (fig. 279).

See Appendix 1 for the locality records of the six specimens examined.

### *Plectrohyla guatemalensis* Brocchi

*Plectrohyla guatemalensis* Brocchi, 1877a, p. 92 [syntypes, M.N.H.N. No 6332 (2 specimens), from Pacicilla (=Patzicia), Departamento Chimaltenango, Guatemala; Marie-Firmin Bocourt collector]. Stuart, 1963, p. 39.

*Cauphias guatemalensis* Brocchi, 1877b, p. 130; 1882, p. 62.

*Hyla guatemalensis*: Boulenger, 1882a, p. 396. Günther, 1901 (1885-1902), p. 281.

**DIAGNOSIS:** This large species (76 mm. snout-vent) has a weakly to strongly tuberculate dorsum. Males have a bifid prepollical spine and lack vocal slits. The only other species with a bifid prepollical spine, *hartwegi*, has dark vertical bars on the flanks and anterior and posterior surfaces of the thighs and dark mottling on the ventral surfaces of the shanks; *guatemalensis* lacks these bold markings. Of the other species lacking vocal slits, *avia* has a single, terminally pointed prepollical spine and a smooth green dorsum, except for small tubercles on the head. *Plectrohyla pycnochila* has a blunt, flat prepollical process, and *lacertosa* is much smaller (47 mm. snout-vent length) and has an elongate, round, terminally blunt prepollical spine. The species possessing vocal slits are smaller (less than 50 mm. snout-vent); each has a single, pointed prepollical spine.

**DESCRIPTION:** Males of this large species attain a maximum known snout-vent length of 76.1 mm., and females reach 73.6 mm. In a series of six adult males from Finca Los Alpes, Departamento Alta Verapaz, Guatemala, the snout-vent length is 72.1 to 76.1 (mean, 73.4) mm.; the ratio of tibia length to snout-vent length is 0.539 to 0.576 (mean, 0.563); the ratio of foot length to snout-vent length is 0.457 to 0.513 (mean, 0.488); the ratio of head length to snout-vent length is 0.274 to 0.292 (mean, 0.285); the ratio of head width to snout-vent length is 0.333 to 0.347 (mean, 0.343), and the ratio of the diameter of the tympanum to that of the eye is 0.240 to 0.357 (mean, 0.304). Five adult females from the same locality have snout-vent lengths of 68.4 to 73.6 (mean, 70.4) mm. and do not differ significantly in proportions from the males. Individuals from the western part of the range, in Chiapas, México, are somewhat smaller than those specimens from Guate-



mala (the eastern part of the range). Furthermore, the specimens from Chiapas have proportionately shorter limbs and a smaller head, but a proportionately larger tympanum. For example, seven adult males from streams above Rayón Mesealapa, Chiapas, México, have snout-vent lengths of 51.2 to 61.5 (mean, 55.9) mm.; the ratio of tibia length to snout-vent length is 0.486 to 0.558 (mean, 0.518); the ratio of foot length to snout-vent length is 0.407 to 0.464 (mean, 0.446); the ratio of head length to snout-vent length is 0.255 to 0.305 (mean, 0.287); the ratio of head width to snout-vent length is 0.291 to 0.363 (mean, 0.327), and the ratio of the diameter of the tympanum to that of the eye is 0.318 to 0.379 (mean, 0.352).

The head is nearly as broad as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded, and in lateral profile it slopes abruptly from the nostrils to the edge of the jaw. The snout is short, its length is equal to the diameter of the eye. The nostrils are barely protuberant and nearly terminal. The canthus is well defined and angular; the loreal region is deeply concave, and the lips are thick and moderately flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. One or two dermal folds extend ventrally from this heavy fold. The fold obscures the upper edge of the tympanum, which in most specimens otherwise is distinct and separated from the eye by a distance equal to more than twice the diameter of the tympanum.

The arms are short and robust; they are especially heavy in breeding males. A few small tubercles are present on the ventrolateral edge of the forearm, and a heavy transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear large discs; the width of the disc on the third finger is more than twice the diameter of the tympanum. The subarticular tubercles are large and subconical; the distal tubercle on the fourth finger is flattened and in some individuals faintly bifid. The supernumerary tubercles are moderately large and conical; they are arranged in a single row on the proximal segments of each digit. A large, diffuse, bifid palmar tubercle is present. The

prepollex is large, elongate, and bifid. The webbing in the hands is vestigial (fig. 273B). The hind limbs are moderately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A heavy transverse dermal fold is present on the heel, and an elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, flat, and elliptical. The outer metatarsal tubercle is small and subconical. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are large and subconical. Moderately large, subconical, supernumerary tubercles are present on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 273E). The webbing extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and onto the base of the disc of the fifth toe.

The anal opening is directed posteroven- trally near the midlevel of the thighs. A short, heavy, anal sheath is present; it has a membranous connection with the skin on the posterior surfaces of the thighs. The skin on the dorsum is smooth or bears small scattered tubercles. The skin on the throat, belly and ventral surfaces of the thighs is granular; that on the ventral surfaces of the arms and shanks is smooth. The tongue is nearly round and barely free behind. The tongue is notched shallowly posteriorly and in all specimens and anteriorly in some specimens. The denticulous processes of the prevomers are narrowly separated, transverse elevations between the posterior margins of the quadrangular choanae. There are three to six teeth on each elevation. The number of teeth on the maxillary and premaxillary (one side only) varies from 32 to 39. Vocal slits and a vocal sac are absent.

The general coloration of *Plectrohyla guatemalensis* is dull green above variously

marked, or not, with shades of brown (pl. 69, fig. 3). Individuals from Alta Verapaz, Guatemala, were primarily dull olive-green above with or without tan or brown markings. The venter was grayish white. One individual from 5.6 kilometers south of Rayón Mescalapa, Chiapas, México, was dull gray above with olive-green spots. The webbing and venter were gray. One specimen from near Panajachél, Sololá, Guatemala, was dark green above with reddish brown markings; the posterior surfaces of the thighs and the webbing were gray. Another specimen from Granja Lorena, Quetzaltenango, Guatemala, had a dull olive-brown dorsum; the flanks and posterior surfaces of the thighs were pale green, and the venter was gray. In all individuals, the iris was golden bronze with or without fine black reticulations.

In preservative, the dorsum is dark brown, bluish black, or dull gray. The venter is dull creamy tan or grayish brown.

**TADPOLES:** A typical tadpole in developmental stage 27 has a body length of 15.2 mm. and a total length of 43.0 mm. The body is ovoid, widest posteriorly, and no wider than deep. In dorsal profile the snout is bluntly rounded, and in lateral profile, it is acutely rounded. The eyes are small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is about on the midline at a point slightly posterior to the midlength of the body. The cloacal tube is long and dextral. The caudal musculature is moderately robust and does not extend to the tip of the rounded tail. The fins are shallow; at midlength of the tail, the caudal musculature is deeper than either the ventral or dorsal caudal fin. The dorsal fin does not extend onto the body (fig. 275F).

The body is dark brown with scattered lichenous markings laterally. The caudal musculature is pale brown, and dark brown flecks and small blotches are present on the musculature and fins. In preservative, the body is dark brown, and the caudal musculature is creamy tan. Faint brown blotches are evident on the musculature and fins.

The mouth is ventral and large; its width

is equal to about two-thirds the width of the greatest width of the body. There is no lateral fold, and the lips are completely bordered by two rows of small papillae. Medial to the fringing rows is a single row of larger papillae; numerous large papillae are present laterally. The beaks are moderately robust and bear short, blunt serrations. The upper beak is in the form of a broad arch with short lateral processes, and the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are long and equal in length; the second upper row is narrowly interrupted medially. The lower rows are complete, moderately long and of equal length (fig. 276F).

Stuart (1942, p. 8) described and illustrated this tadpole as "Form x."

**MATING CALL:** The absence of vocal slits and a vocal sac precludes the presence of a mating call in this species.

**NATURAL HISTORY:** *Plectrohyla guatemalensis* is an inhabitant of cloud forest and humid pine-oak forest. At Finca Los Alpes, Guatemala, adults were found on vegetation overhanging streams by day and by night. At the same locality, individuals were found sitting on rocks behind the waterfall, in a hole in a cliff behind a waterfall, and on rocks in the streams at night. On cloudy or rainy days, these frogs frequently are active; at these times they can be found perched on rocks or vegetation in or along cascading mountain streams.

Tadpoles in various stages of development have been found throughout most of the year. Thus, it seems likely that this species has no definite breeding season. Metamorphosing young were found at Finca Los Alpes on July 31, 1961, and along a stream 6.2 kilometers south of Rayón Mescalapa, Chiapas, on June 16, 1960. Stuart (1954e, p. 48) found three subadults in a bromeliad in a tree overhanging a nearly dry stream where tadpoles were present at San Lorenzo, Guatemala, in mid-February.

Recently metamorphosed young having snout-vent lengths of 23.0 and 24.4 mm. were pale olive-green above with pale green blotches posterolaterally; the throat and chest were silvery green.

**REMARKS:** *Plectrohyla guatemalensis* oe-

eurs sympatrically with several other species of the genus (*avia*, *matudai*, *sagorum*, *quecchi*, and *ixil*). *Plectrohyla guatemalensis* and *avia* tend to frequent the larger streams than do the smaller species (*matudai*, *sagorum*, *quecchi*, and *ixil*), which often inhabit rivulets.

**ETYMOLOGY:** The specific name refers to Guatemala, country of origin of the type specimen.

**DISTRIBUTION:** *Plectrohyla guatemalensis* occurs at elevations from 1000 to 2800 meters on the Atlantic slope of the highlands of Chiapas and Guatemala eastward to the Sierra de Nombre de Dios in north-central Honduras; on the Pacific slopes, the species occurs from south-central Chiapas eastward to northern El Salvador (fig. 280).

See Appendix 1 for the locality records of the 103 specimens examined.

#### *Plectrohyla hartwegi* Duellman

*Plectrohyla hartwegi* Duellman, 1968a, p. 576 [holotype, U.M.M.Z. No. 94428 from Barrejón, 19 kilometers west of Chicomuselo, Chiapas, México, 1000 meters; Eizi Matuda collector].

**DIAGNOSIS:** This moderately large species (64 mm. in snout-vent length) has a bifid prepollex and a tuberculate dorsum. *Plectrohyla hartwegi* differs from all other members of the genus by having bold bars on the flanks and anterior and posterior surfaces of the thighs, and dark mottling on the ventral surfaces of the shanks.

**DESCRIPTION:** Males of this species attain a maximum known snout-vent length of 63.8 mm.; the females are unknown. Three males have snout-vent lengths of 41.8 to 63.8 (mean, 51.3) mm.; the ratio of tibia length to snout-vent length is 0.547 to 0.579 (mean, 0.558); the ratio of foot length to snout-vent length is 0.464 to 0.487 (mean, 0.475); the ratio of head length to snout-vent length is 0.309 to 0.339 (mean, 0.332); the ratio of head width to snout-vent length is 0.350 to 0.377 (mean, 0.360), and the ratio of the diameter of the tympanum to that of the eye is 0.426 to 0.473 (mean, 0.445).

The head is as broad as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is angular and slopes abruptly from

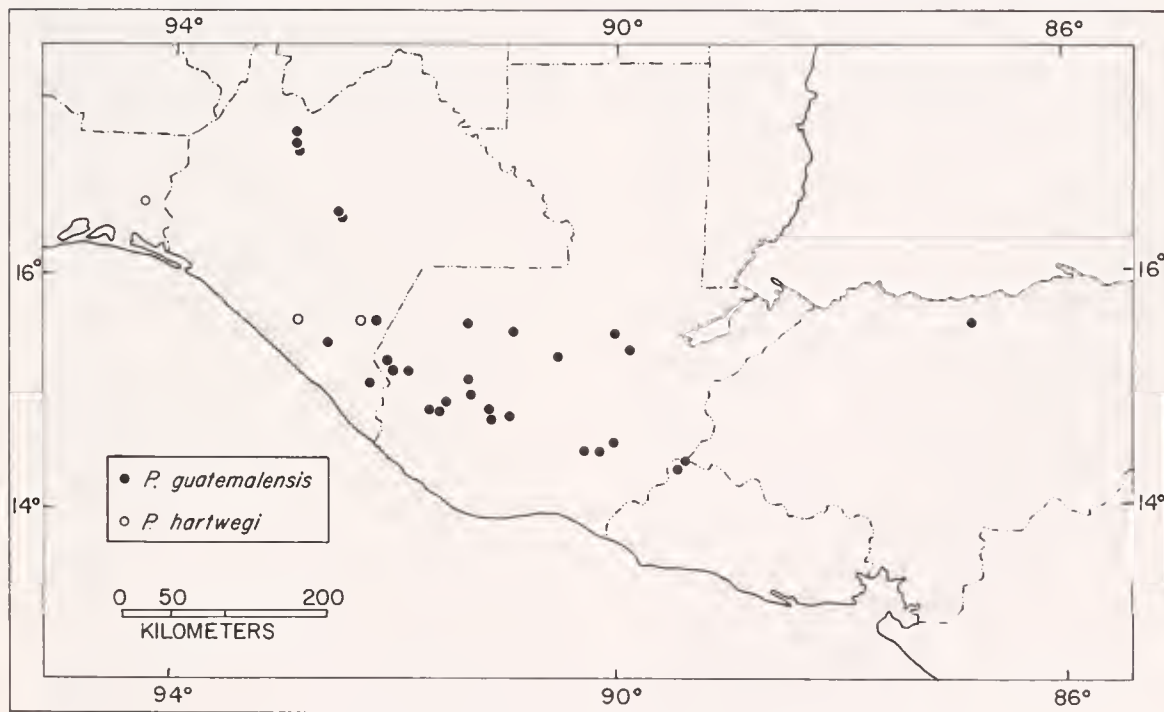


FIG. 280. Distribution of *Plectrohyla guatemalensis* and *Plectrohyla hartwegi*.



the nostrils to the jaw. The snout is short, and the nostrils are barely protuberant and situated at a point about two-thirds of the distance from the eyes to the tip of the snout. A heavy dermal fold extends from the eye, above the tympanum, and downward to a point above the insertion of the arm. Two thinner folds extend ventrally from the heavy fold and cover the posterior edge of the tympanum. The anterior and ventral edges of the tympanum are distinct, and the tympanum is separated from the eye by a distance equal to the diameter of the tympanum.

The arms are robust. There is no distinct row of tubercles on the ventrolateral edge of the forearm, but there is a faint transverse dermal fold present on the wrist. The fingers are long and moderately slender and bear large discs, the width of the disc on the third finger is noticeably greater than the diameter of the tympanum. The subarticular tubercles are small and conical; except the distal tubercle on the fourth finger, which is somewhat flattened (bifid in one specimen). The supernumerary tubercles are small, subconical, and arranged in one row on the proximal segment of the fourth finger and in two rows on the proximal segments of the other fingers. Two small palmar tubercles are present. The prepollex is greatly enlarged, barely bifid, and does not have spines protruding through the skin. The webbing on the hands is vestigial (fig. 273C). The hind limbs are moderately long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends slightly beyond the tip of the snout. A heavy transverse dermal fold is present on the heel, and a heavy tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is high, elliptical, and visible from above. The outer metatarsal tubercle is absent. The toes are long and slender and bear rather small discs. The subarticular tubercles are small and round; the supernumerary tubercles are small and arranged in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 273F). The webbing extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, to the base of the disc

of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. The anal sheath is long and has a membranous connection to the posterior surfaces of the thighs. The skin on the dorsal surfaces is finely tuberculate; that on the throat, chest, belly, and posteroventral surfaces of the thighs is granular, whereas the skin on the ventral surfaces of the arms and shanks is smooth. The tongue is nearly round and free posteriorly for about one-fourth of its length; it is marginate or barely notched behind. The denticerous processes of the prevomers are small elliptical elevations between the quadrangular choanae. There are four or five teeth on each process. The number of maxillary and premaxillary teeth (one side only) varies from 35 to 40. Vocal slits and a vocal sac are absent.

The coloration in life is unknown. In preservative, the dorsum is uniformly dull brown. The flanks are brown with creamy yellow mottling and dark brown spots in the groin; the anterior surfaces of the thighs are creamy yellow with broad, vertical, dark brown bars proximally and narrower dull brown bars distally. The posterior surfaces of the thighs are brown with dark brown vertical bars (pl. 5, fig. 2). The belly and ventral surfaces of the limbs are creamy yellow; bold brown reticulations are present on the ventral surfaces of the shanks.

**TADPOLES:** The tadpoles of this species are unknown.

**MATING CALL:** The absence of vocal slits and presumably a vocal sac probably precludes the presence of a voice in this species.

**NATURAL HISTORY:** One specimen obtained in May on Parajé El Triunfo was found in a rocky stream in the cloud forest at an elevation of 2050 meters. There is no other available information on the natural history of this species.

**REMARKS:** On the basis of the general shape of this frog and the presence of a bifid prepollex, it seems logical to associate this species as a relative of *Plectrohyla guatema-*

*lensis*, from which it differs chiefly in color pattern. The geographic ranges of the two species overlap; consequently, it is highly unlikely that *hartwegi* represents a geographic race of *guatemalensis*.

**ETYMOLOGY:** The specific name is a patronym for Norman Hartweg, who first recognized the distinctness of this species.

**DISTRIBUTION:** *Plectrohyla hartwegi* is known from elevations of 1000 to 2050 meters on the Pacific slopes of the Sierra Madre in Chiapas and extreme eastern Oaxaca, México (fig. 280).

See Appendix 1 for the locality records of the three specimens examined.

### Genus *Smilisca* Cope

*Smilisca* Cope, 1865b, p. 194 [type species, *Smilisca daulinia* Cope, 1865 = *Hyla baudinii* Duméril and Bibron, 1841].

**GENEROTYPE:** *Hyla baudinii* Duméril and Bibron, 1841. Cope (1865b, p. 194) in his synopsis of the genera of hylid frogs based the diagnosis of the genus *Smilisca* on a "skeleton in the private anatomical museum of Hyrtl, Professor of Anatomy in the University of Vienna." Cope referred to the specimen as *Smilisca daulinia*. Duellman and Trueb (1966, p. 297) suggested that Cope inadvertently used *daulinia* (a new name) for *baudinii* just as he later used *daulinii* for *baudinii* (1871, p. 205). Cope's description of the cranial characters of Hyrtl's specimen leaves no doubt that he had before him a specimen of *Smilisca baudinii*.

**ETYMOLOGY:** The generic name is derived from the Greek *smile*, meaning knife, and the Greek *iskos*, a diminutive suffix, and means literally "little knife" in reference to the sharply pointed frontoparietal processes of *S. baudinii* used as a diagnostic character of the genus by Cope.

**DEFINITION:** Frogs of the genus *Smilisca* are medium to large in size and have a blotched or barred dorsal pattern of shades of green or brown. The flanks are mottled, spotted, or venated, and the venter is creamy white, except for dark colored vocal sacs in most species. The pupil is horizontally elliptical, and the iris is a bronze color with black flecks or reticulations. The palpebral mem-

brane is unmarked. The amount of webbing on the hand is variable, but the toes are at least three-fourths webbed. The first toe is shorter than the second and not opposable to the others. The vocal sacs are paired, subgular, and greatly distensible. The skin on the dorsum is smooth; distinct paratoid glands are lacking. The tongue is ovoid, barely free behind, and variously notched or not. Breeding males have horny brown nuptial excrescences on the thumbs. The skull is broad, well ossified, has a minimal amount of cartilage and/or secondarily ossified cartilage, and lacks dermal co-ossification. An internasal septum and quadratojugals are present. The sphenethmoid is large, and the nasals are moderately slender, separated medially, and separated or not from the sphenethmoid. A frontoparietal fontanelle is present, except in *S. phacota*. Extensive, laterally projecting, frontoparietal processes are present in *S. baudinii* and *phacota*. A well-developed squamosal minimally extends one-fourth of the distance to the maxillary and maximally is in contact with the maxillary. The dentigerous processes of the prevomers are short, widely separated, and situated at a slight angle to the midline. Teeth are present on the premaxillaries, maxillaries, and prevomers, but absent from the palatines and parasphenoid. The teeth are spatulate and strongly bifid. The depressor mandibulae muscle consists of two parts, one arising from the dorsal fascia and the other from the posterior arm of the squamosal. The adductor mandibulae muscle consists of two branches—the posterior subexternus and the externus superficialis. The mandibular branch of the trigeminal nerve passes between the branches of the adductor mandibulae muscle. The tadpoles are generalized and have two upper and three lower rows of teeth, and unspecialized beaks. The mouth is partly or completely bordered by one or two rows of papillae, and the lips are infolded laterally. The spiracle is sinistral, and the cloacal tube is dextral. The caudal musculature extends nearly to the tip of the tail. The mating call consists of one or more short, poorly modulated, explosive notes. The haploid chromosome number is 12, and the diploid number is 24.

COMPOSITION OF GENUS: Six species are currently recognized. All are considered to be monotypic. All known species occur in Middle America. Of the six species, 4544 preserved frogs, 95 skeletons, 95 lots of tadpoles, and five preserved clutches of eggs were examined from Middle America.

ANALYSIS OF CHARACTERS: On the basis of size alone the species fall into two groups; *baudinii*, *cyanosticta*, and *phaeota*, are large, and *puma*, *sila*, and *sordida* are small. The largest specimen examined is a female *baudinii* having a snout-vent length of 90 mm. *Smilisca puma* is the smallest species; the largest male has a snout-vent length of 38 mm. and the largest female, 46 mm. Few significant differences in proportions exist between the species (table 56). *Smilisca baudinii* is more squat and stocky than the other species and has proportionately shorter hind limbs. Although considerable variation in the size of the tympanum exists within each species, noticeable differences are present between species.

Consistent differences exist in relative lengths of the digits, size of the subarticular tubercles, size and number of the supernumerary tubercles, size and shape of the inner metatarsal tubercle, and the amount of webbing (figs. 281-283). In the series of large species (*baudinii*-*phaeota*-*cyanosticta*) a progressive increase in the amount of webbing

in the hand and a decrease in number, and corresponding increase in size, of the supernumerary tubercles are evident. *Smilisca puma* is unique in the genus by lacking webbing in the hand and by having large subarticular tubercles on the hand and a relatively small inner metatarsal tubercle. *Smilisca sila* and *sordida* have shorter, more robust fingers than the other species. Both species have extensive webbing and many small supernumerary tubercles on the feet.

The color and pattern are among the most important taxonomic characters in the genus. Especially significant is the coloration of the flanks, which is venated in *phaeota*, mottled in *baudinii*, venated anteriorly and mottled posteriorly in *puma*, and spotted or flecked in the other species (pls. 70 and 71). *Smilisca cyanosticta* and *phaeota* each has a broad white labial stripe, and *puma* has a narrow stripe. The upper lip is marked with vertical dark bars in *baudinii* and *sila*, whereas it is unicolor in *sordida*. A large dark brown or black postorbital mark is present in *baudinii*, *cyanosticta*, and *phaeota* and absent in the other species. All species have dark transverse bands on the limbs. The dorsum of the body in *puma* is marked by two longitudinal dark stripes that are interconnected in some specimens; the dorsal markings usually consist of one or more irregular dark blotches in the other species, but in some specimens of

TABLE 56  
Comparison of Sizes and Certain Proportions, with Means in Parentheses, of Males of the Species of *Smilisca*.

Species	N	Snout-vent Length	Tibia Length/ S-V L	Tympanum/ Eye
<i>S. baudinii</i> .....	140	47.3-75.9 (58.7)	0.421-0.536 (0.478)	0.561-0.944 (0.735)
<i>S. cyanosticta</i> .....	40	44.6-57.8 (50.7)	0.519-0.597 (0.560)	0.627-0.884 (0.714)
<i>S. phaeota</i> .....	50	40.8-65.5 (53.9)	0.509-0.602 (0.555)	0.627-0.855 (0.766)
<i>S. puma</i> .....	20	31.9-38.1 (34.7)	0.482-0.531 (0.513)	0.521-0.722 (0.649)
<i>S. sila</i> .....	33	31.6-44.8 (37.7)	0.497-0.581 (0.548)	0.476-0.483 (0.532)
<i>S. sordida</i> .....	55	31.9-44.6 (37.9)	0.505-0.571 (0.534)	0.465-0.571 (0.491)



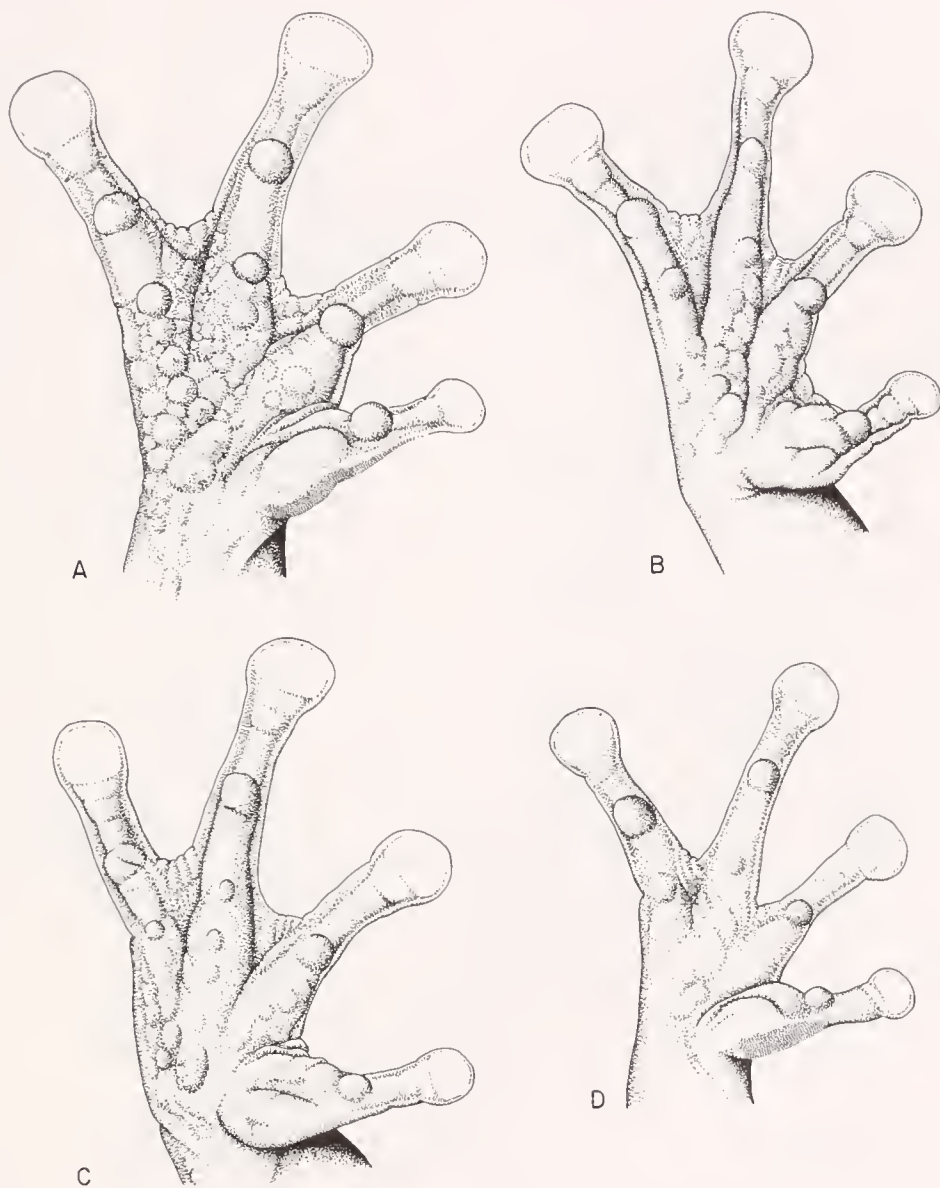


FIG. 281. Hands of four species of *Smilisca*. A. *S. baudinii*, K.U. No. 87182. B. *S. cyanosticta*, K.U. No. 87199. C. *S. phacota*, K.U. No. 96156. D. *S. puma*, K.U. No. 64312.  $\times 4$ , except D, which is  $\times 5$ .

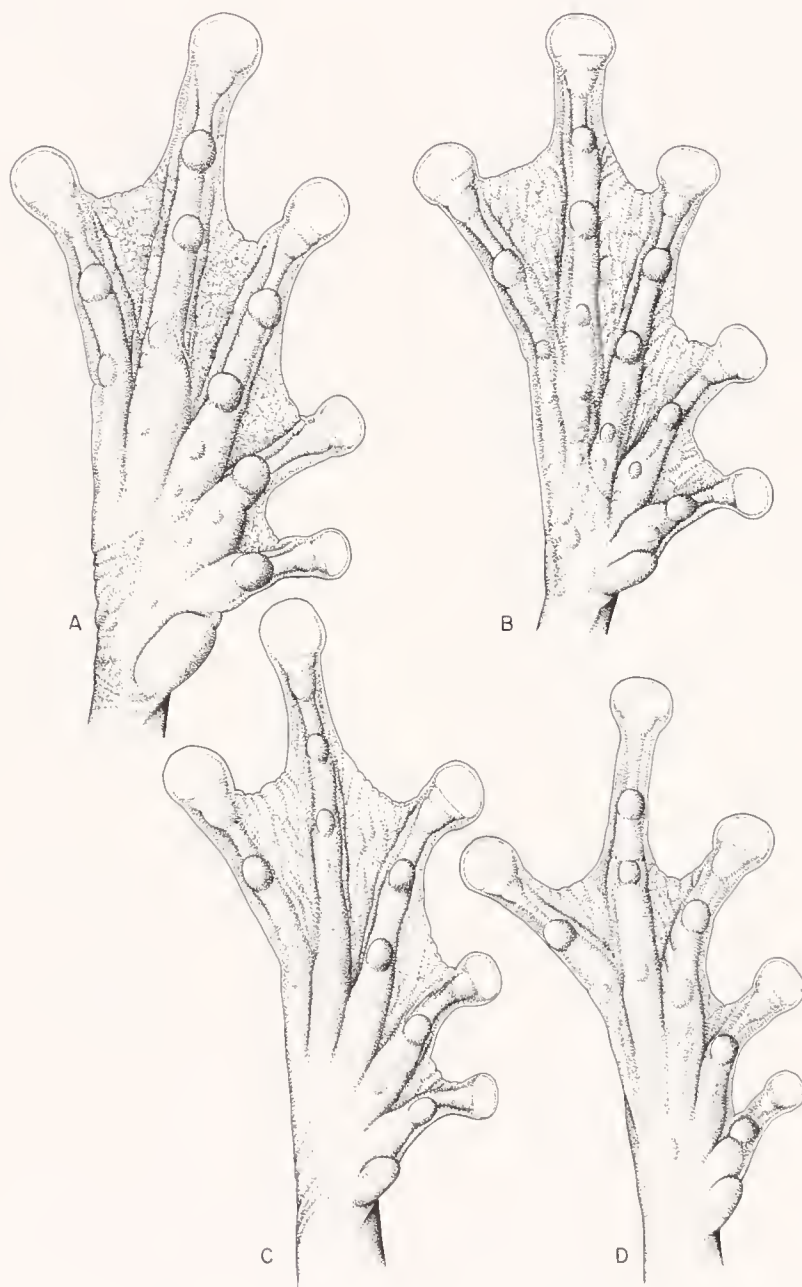


FIG. 282. Feet of four species of *Smilisca*. A. *S. baudinii*, K.U. No. 87182. B. *S. cyanosticta*, K.U. No. 87199. C. *S. phacota*, K.U. No. 96156. D. *S. puma*, K.U. No. 64312.  $\times 4$ , except D, which is  $\times 5$ .

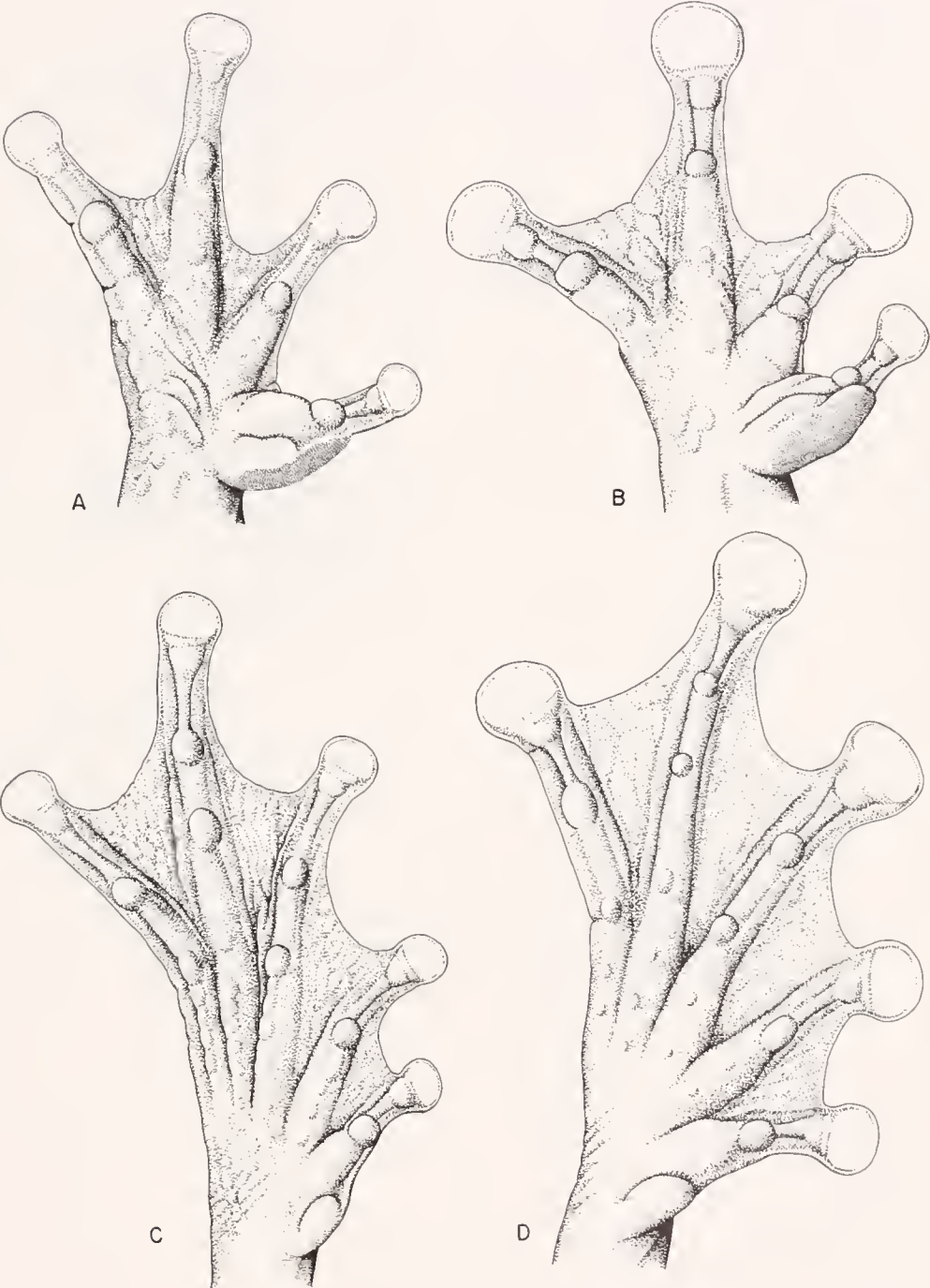


FIG. 283. Hands and feet of two species of *Smilisca*. A and C. *S. sila*, K.U. No. 91867. B and D. *S. sordida*, K.U. No. 91753.  $\times 5$ .



*sordida* the dark marks form transverse bars. The belly is creamy white in all species; the vocal sac is white in breeding *sordida* and gray or brown in the other species.

The tadpoles of *Smilisca sila* and *sordida* live in streams and have ventrally oriented, larger mouths and proportionately longer tails than do the pelagic, pond dwelling tadpoles of the other species (fig. 284). The differences in coloration and in the mouthparts are slight; *Smilisca sordida* is unique in having two complete rows of labial papillae and long, shallowly S-shaped lateral processes on the upper beak (fig. 285).

Examination of the skulls reveals that members of the *baudinii* group (*baudinii*, *cyanosticta*, and *phaeota*) have well ossified skulls that have gently curved lateral margins and relatively large nasals with their long axes parallel to the maxillaries. Anteriorly the nasals are pointed and posteriorly they bear long, delicate palatine processes extending to the maxillaries. The sphenethmoid is fully ossified and extends anteriorly between the nasals. The squamosals are large and extend to the maxillary in *baudinii*, but not in *cyanosticta* and *phaeota*. The prootics are massive. Extensive lateral flanges are present on the frontoparietals in *baudinii* and *phaeota* (fig. 286). The skulls of *puma* and *sordida* differ from those of the *baudinii* group by having somewhat angular lateral margins, small bony sphenethmoid that does not extend anteriorly between the nasals, and relatively small prootics. The moderate-sized nasals are rounded anteriorly and bear relatively short maxillary processes; the long axes of the nasals are not parallel to the maxillaries. The squamosals are small and do not extend to the maxillaries (fig. 286). The skull of *Smilisca sila* is intermediate between these two species groups. The lateral margins are gently curved but have a pronounced angularity just anterior to the palatines. The nasals are moderate in size and have their long axes parallel to the maxillaries. The nasals are slightly pointed anteriorly and bear short, blunt palatine processes posteriorly. The sphenethmoid is extensively ossified but does not extend anteriorly between the nasals. The prootics are relatively large but short. The squamosals are moderate in size; the anterior

arms extend only one-fourth the distance to the maxillary. Duellman and Trueb (1966) discussed the comparative osteology of the species of *Smilisca* in detail, and Trueb (1968b) described the internal cranial anatomy of *S. baudinii*.

The mating calls of all species of *Smilisca* consist of short, explosive, poorly modulated notes. The calls consist of one "wonk" of series of such notes in *baudinii* and *cyanosticta*, a low growl in *phaeota*, and a relatively high-pitched rattle in *sordida*. The calls of *puma* and *sila* consist of a low-pitched squawk usually followed by one or more rattling secondary notes. Quantitatively, the calls of the species differ in the number of notes, duration of notes, and in pitch (table 57, pls. 32 and 33).

**DISTRIBUTION:** The combined distributions of the six species of *Smilisca* include most of the lowlands of México and Central America, in some places to elevations of nearly 2000 meters. The range extends from southern Sonora, México, and the Río Grande Embayment of Texas to South America and includes such continental islands as Isla Cozumel, México, Isla Roatan, Honduras, and Isla Popa and Isla Cébaco in Panamá. In South America one species occurs on the Caribbean lowlands of Colombia and in the valleys of the Río Cauca and Río Magdalena; another species occurs on the Pacific slopes of Colombia and northwestern Ecuador.

**DISCUSSION:** The genus *Smilisca* has not been consistently recognized by workers in the past twenty years. Except for Cope's various publications dealing with the Neotropical herpetofauna, the name was not used in the 1800's. Smith and Taylor (1948) resurrected the generic name and followed Cope by only including *Hyla baudinii* Duméril and Bibron in the genus. Starrett (1960b) expanded the definition of the genus and placed *Hyla gabbi* Cope, *Hyla phaeota* Cope, and *Hyla wellmanorum* Taylor in the genus. Duellman and Trueb (1966) refined the definition of the genus and recognized the six species that are currently placed in the genus.

Although *Smilisca* is difficult to define, the six included species seem to form a natural group. The paired subgular vocal sacs are a reliable diagnostic character. Experience



FIG. 284. Tadpoles of the species of *Smilisca*. A. *S. baudinii*, K.U. No. 60018. B. *S. cyanosticta*, K.U. No. 87652. C. *S. phaeota*, K.U. No. 87683. D. *S. puma*, K.U. No. 91807. E. *S. sila*, K.U. No. 80620. F. *S. sordida*, K.U. No. 68475.  $\times 4.5$ .

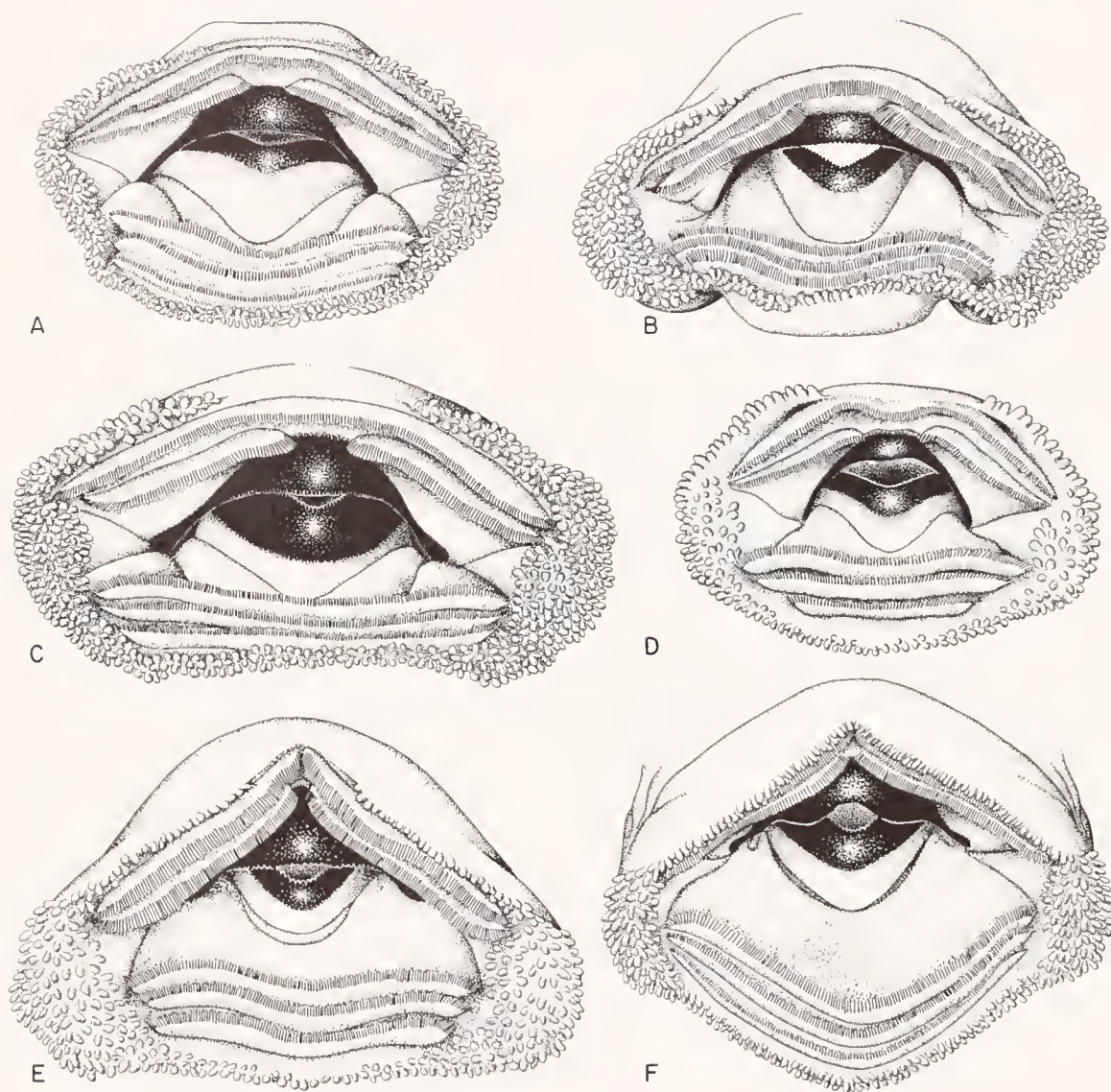


FIG. 285. Mouths of tadpoles of the genus *Smilisca*. A. *S. baudinii*, K.U. No. 60018. B. *S. cyanosticta*, K.U. No. 87652. C. *S. phacota*, K.U. No. 87683. D. *S. puma*, K.U. No. 91807. E. *S. sila*, K.U. No. 90620. F. *S. sordida*, K.U. No. 68475. All  $\times 25$ , except F, which is  $\times 17$ .



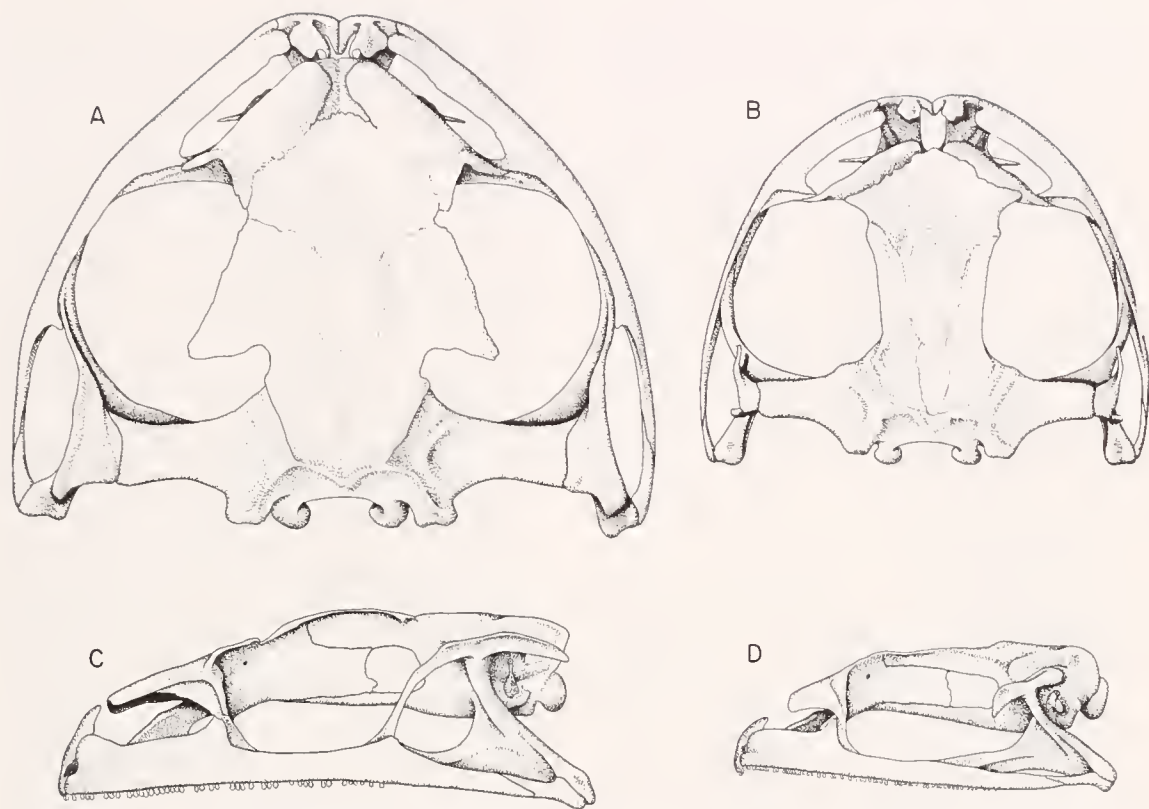


FIG. 286. Dorsal and lateral views of the skulls of *Smilisca*. A and B. *S. phaeota*, K.U. No. 91827. C and D. *S. sordida*, K.U. No. 34872.  $\times 3$ .

TABLE 57

Characteristics of the Mating Calls, with Means in Parentheses, of the Species of *Smilisca*.

Species	N	Notes per Call Group	Duration of Note (seconds)	Fundamental Frequency (cps)	Major Frequencies (cps)	
					Lower	Upper
<i>S. baudinii</i> .....	20	2-15 (8.0)	0.09-0.13 (0.11)	135-190 (166.2)	175-495 (351)	2400-2725 (2507)
<i>S. cyanosticta</i> .....	10	1-2 (1.2)	0.25-0.45 (0.38)	135-160 (145.1)	480-935 (841)	1600-2100 (1894)
<i>S. phaeota</i> .....	10	1-2 (1.6)	0.10-0.45 (0.31)	110-165 (143.0)	330-495 (372)	.....
<i>S. puma</i> .....	28	2-10 (3.7)	0.06-0.35 (0.13)	125-200 (145.6)	495-980 (743)	1456-2240 (1868)
<i>S. sila</i> .....	15	1-6 (2.4)	0.06-0.28 (0.16)	90-115 (103.0)	665-1180 (889)	1980-2700 (2218)
<i>S. sordida</i> .....	19	1-6 (1.7)	0.18-0.45 (0.29)	90-140 (123.1)	1150-1540 (1216)	2340-2990 (2694)

with the frogs in the field substantiates the close relationship of the six species. The mating calls, behavior, and general habitus are sufficiently alike so as to remove doubts about their relationships.

By utilizing internal and external morphological characters, larval characters, mating calls, and analyses of skin proteins, Duellman and Trueb (1966) divided the genus into two species groups. The *baudinii* group contains the three large species (*baudinii*, *cyanosticta*, and *phaeota*), and the *sordida* group contains the three small species (*puma*, *sila*, and *sordida*). The reader is referred to Duellman and Trueb (1966) for a detailed discussion of the phylogenetic relationships and a reconstruction of the phylogenetic history.

### *Smilisca baudinii* (Duméril and Bibron)

*Hyla baudinii* Duméril and Bibron, 1841, p. 564 [holotype, M.N.H.N. No. 4798 from "Mexique"; Baudin collector; type locality restricted to Córdoba, Veracruz, México, elevation 925 meters by Smith and Taylor (1950)]. Brocchi, 1882, p. 29. Boulenger, 1882a, p. 371. Günther, 1901 (1885-1902), p. 270. Kellogg, 1932, p. 160.

*Hyla vanlietii* Baird, 1854, p. 61 [holotype, U.S.N.M. No. 3256 from Brownsville, Cameron County, Texas, elevation 15 meters; Captain S. Van Vliet collector].

*Hyla vociferans* Baird 1859, p. 35 [figures 11-13 on plate 38 are designated "*Hyla vociferans*, Baird"; the name is not mentioned in the text, nor is a specimen designated].

*Hyla muricolor* Cope, 1862, p. 359 [holotype, U.S.N.M. No. 25097 from Hacienda Mirador, Veracruz, México, elevation 1020 meters; Charles Sartorius collector].

*Smilisca daulinia* (lapsus for *baudinii*) Cope, 1865b, p. 194.

*Smilisca daudinii* (lapsus for *baudinii*) Cope, 1871, p. 31.

*Smilisca baudinii*: Cope, 1875, p. 31. Taylor, 1952c, p. 794. Stuart, 1963, p. 41. Duellman and Trueb, 1966, p. 289.

*Hyla pansosana* Brocchi, 1877b, p. 125 [holotype, M.N.H.N. No. 6313 from Panzós, Alta Verapaz, Guatemala, elevation 36 meters; Marie-Firmin Bocourt collector].

*Hyla baudinii* (*bandinii* by fiat): Barbour, 1923, p. 11.

*Hyla baudinii baudinii*: Stejneger and Barbour, 1923, p. 34.

*Hyla beltrani* Taylor, 1942d, p. 306 [holotype, U.I.M.N.H. No. 25046 from Tapachula, Chiapas, México, elevation 140 meters; A. Magaña collector].

*Smilisca baudinii baudinii*: Smith, 1947, p. 408. Smith and Taylor, 1948, p. 75.

*Hyla manisorum* Taylor, 1954b, p. 630 [holotype, K.U. No. 34927 from Batán, Limón Province, Costa Rica, elevation 15 meters; Edward H. Taylor collector].

**DIAGNOSIS:** This large member of the genus is readily discernible from other *Smilisca* by the presence of a large, high, elliptical inner metatarsal tubercle, a short, bluntly rounded snout, relatively short hind limbs (tibia length is less than 55 per cent of the snout-vent length), contrasting dark vertical bars on the upper lip, a broad postorbital dark mark, cream flanks with bold brown or black reticulations in the groin, the posterior surfaces of the thighs brown with cream flecks, and the dorsal surfaces of the limbs marked with dark transverse bands. The dorsum is variously marked with large spots or blotches, and in breeding males the vocal sacs are gray. Other members of the *Smilisca baudinii* group (*cyanosticta* and *phaeota*) have a low, flat, elliptical inner metatarsal tubercle, a more pointed snout, relatively longer hind limbs, and a white labial stripe. Furthermore, the flanks in *phaeota* are pale cream with a brown or black venated pattern, and the flanks and thighs in *cyanosticta* are dark brown with pale blue or green spots. The only other *Smilisca* with a short truncate snout is the much smaller (maximum size of males, 45 mm., of females, 62.2 mm.) *S. sila*, which has blue spots or flecks on the flanks and posterior surfaces of the thighs.

**DESCRIPTION:** *Smilisca baudinii* is the largest species in the genus; males attain a maximum snout-vent length of 76 mm., and females reach 90 mm. The size attained by adults of both sexes varies geographically. The largest specimens are from Sinaloa (mean snout-vent length of males, 68.6 mm.); those from the Atlantic lowlands of Alta Verapaz in Guatemala, Honduras, and Costa Rica are somewhat smaller, whereas those from the Pacific lowlands of Central America are smaller still. The smallest breeding males are from Isla del Carmen, Campeche, México (mean snout-vent length, 50.9 mm.).

In a sample of 25 males from Esparta, Puntarenas Province, Costa Rica the snout-vent length is 53.3 to 66.0 (mean, 60.2) mm. The ratio of the tibia length to the snout-

vent length is 0.451 to 0.520 (mean, 0.482); the ratio of the foot length to snout-vent length is 0.422 to 0.489 (mean, 0.448), the ratio of head length to snout-vent length is 0.300 to 0.342 (mean, 0.320); the ratio of head width to snout-vent length is 0.344 to 0.383 (mean, 0.361), and the ratio of the diameter of the tympanum to that of the eye is 0.679 to 0.911 (mean, 0.777). Considerable variation in certain proportions is evident from samples selected from throughout the range, but no geographic trends are apparent. Specimens from Sinaloa in northwestern México have the largest tympani (mean tympanum/eye ratio, 0.878); the next highest ratio (0.794) is in frogs from Managua, Nicaragua, whereas frogs from intermediate localities have smaller tympani (ratio at Ocotito, Guerrero, México, 0.746). Similar discordant variation occurs in the relative length of the hind limb. The mean ratio of tibia length to snout-vent length is 0.512 and 0.515 in Limón Province, Costa Rica, and in Departamento Atlantida, Honduras, respectively; the ratio is 0.449 in specimens from San Salvador, El Salvador, and from southern Sinaloa, México. The ratios are intermediate in frogs from other localities. See Duellman and Trueb (1966) for further data on geographic variation in size and proportions.

The head is about as wide as the body and is wider than long. The top of the head is flat. In dorsal profile the snout is acutely rounded; in lateral profile the snout is bluntly rounded. The snout is moderately short. The nostrils are slightly protuberant and are situated at about three-fourths the distance from the eyes to the tip of the snout. The canthus is rounded and distinct; the loreal region is noticeably concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extending posteriorly from the posterior corner of the eye to a point above the insertion of the arm conceals the upper edge of the tympanum in some specimens. Otherwise the tympanum is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arm is moderately long; the upper arm is slender, and the forearm is robust. No axillary membrane is present. A row of low

tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse fold is present on the wrist. The fingers are moderately long and stout and bear moderately large discs. The width of the disc on the third finger nearly equals the diameter of the tympanum. The subarticular tubercles are small and conical; the distal tubercle on the fourth finger is flattened and in about half of the specimens is bifid. The supernumerary tubercles are small, conical, and distinct. Usually they are in two rows on the proximal segment of each finger, except the third, where they are in three or four rows. A tripartite palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrecence. The fingers are about one-third webbed (fig. 281A). A trace of web exists between the first and second fingers; the web extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third and from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are short and heavy; the adpressed heels barely overlap, and the tibiotarsal articulation extends to a point between the tympanum and the eye. A heavy tarsal fold extends the length of the tarsus. The inner metatarsal tubercle is large, high, and elliptical. The shape of the tubercle varies from an elongate ellipse with rounded edges to a spade-like structure. The tubercle is most pronounced in specimens from northwestern México, Tamaulipas, and the Pacific lowlands of Central America. The toes are moderately long and broad; the discs are noticeably smaller than those on the fingers. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, conical, and in a single row of each toe. The toes are about three-fourths webbed (fig. 282A). The web extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.



The anal opening is directed posteroventrally near the upper level of the thighs and is covered by a short anal sheath. The skin is granular on the belly and ventral surfaces of the thighs; other surfaces are smooth. The tongue is cordiform, shallowly notched anteriorly and posteriorly, and barely free behind. There are five to nine (mean, 7.2) prevomerine teeth on high transverse ridges between the quadrangular choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is paired, subgular, and greatly distensible.

The general coloration of *Smilisca baudinii* is pale green with olive-green markings, olive-green with brown markings, or pale brown with dark brown markings (pl. 70, figs. 4 and 5). The markings on the back consist of irregular spots or blotches. In most specimens a dark interorbital bar is present and usually connected to a large dorsal blotch. The limbs are marked with dark transverse bands, usually three each on the forearm and thigh and three or four on the shank. Transverse bands also are present on the tarsi and proximal segments of the fingers and toes. The dorsal markings are usually outlined with black. A dark brown canthal stripe is present. The loreal region and upper lips are pale green or tan; the upper lip usually is boldly marked with vertical dark brown bars. Especially evident is a bar below the eye; the pale area just posterior to this bar is creamy white or ashy gray in some specimens. A dark brown or black mark extends from the tympanum to a point above the insertion of the arm. In most specimens this mark is broad and distinct, but in some it is restricted to a narrow stripe immediately below the posterior part of the supratympanic fold. The flanks are yellow or cream with brown or black mottling; in some specimens the dark mottling encloses pale spots, especially in the groin. The anterior surfaces of the thighs are colored like the flanks, except that the mottling is weaker; the posterior surfaces of the thighs are brown with small creamy yellow spots. A distinct creamy white anal stripe usually is present. White stripes along the outer edges of the tarsi and forearms usually are absent. In most specimens the venter is white, but in specimens from the

Atlantic slopes and lowlands of Guatemala the belly, especially posteriorly, is yellow. In breeding males the throat is gray. The iris varies from golden bronze to dull bronze with black reticulations.

Although considerable variation in color and pattern exists, the variation does not seem to be closely correlated with geography. In specimens from the southern part of the range the dorsal dark markings usually are in the form of small spots, especially on the posterior part of the body. Two specimens from Limón Province, Costa Rica (K.U. No. 34927 from Batán and K.U. No. 36789 from Suretka), lack a dorsal pattern and bands on the limbs. These specimens are nearly uniform brown above with only a few small dark spots on the back. Six specimens (K.U. Nos. 78464, 78466-78470 from 7.3 kilometers southwest of Matatán, Sinaloa, México) are distinctive in having a uniformly grayish green dorsum with the only dorsal marks being on the tarsi; canthal and post-tympanic dark marks are absent, and a broad white labial stripe is present and interrupted by a single vertical dark mark below the eye. Furthermore, a white stripe is present along the outer edge of the foot, and the flanks and posterior surfaces of the thighs are creamy white, boldly marked with black.

Throughout most of the range the lips are strongly barred, but in some specimens from southern Nicaragua and Costa Rica the lips are pale, and in a few specimens the vertical bars are indistinct. Two specimens from Departamento Alta Verapaz, Guatemala (F.M.-N.H. No. 21006 from Cobán and U.M.M.Z. No. 90908 from Finca Canihor) differ by having many narrow transverse bands on the limbs and fine reticulations on the flanks.

In preservative the dorsum varies from pale bluish gray to brown or tan with darker markings. The yellow spots on the flanks and posterior surfaces of the thighs fade to creamy white.

**TADPOLES:** Ten hatchlings (developmental stage 21) have total lengths of 5.1 to 5.4 (mean, 5.22) mm.; 10 tadpoles in developmental stage 38 have total lengths of 35.0 to 37.5 (mean, 35.5) mm. The relative length of the tail to the length of the body increases greatly from the time of hatching until re-

sorption begins at developmental stage 40. The average ratio of tail length to total length in hatchlings is 0.495, whereas in stage 38 the ratio is 0.640.

A typical tadpole in developmental stage 30 has a total length of 22.3 mm. The body is slightly wider than deep; the snout is round in dorsal and lateral profiles. The nostrils are about midway between the eyes and the tip of the snout. The eyes are widely separated and directed dorsolaterally. The spiracle is sinistral and slightly ventral to the midline, and the spiracular opening is at about midlength of the body. The mouth is anteroventral; the cloacal tube is short and dextral. The caudal musculature is slender, slightly curved upward distally, and does not quite reach the tip of the tail. The dorsal fin extends onto the body and is deepest at about one-third the length of the tail. At midlength of the tail the dorsal fin is slightly deeper than the ventral fin (fig. 284A).

The mouth is moderately small and has well-developed lateral folds. The median part of the upper lip is bare; the rest of the mouth is bordered by two rows of labial papillae, except that additional papillae are present in the lateral fold. The upper beak is moderately deep and forms a broad arch with slender lateral processes. The lower beak is more slender and broadly V-shaped; both beaks have blunt serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length, and the second row is broadly interrupted medially. The three lower rows are complete; the first and second rows are equal in length and slightly shorter than the upper rows, whereas the third lower row is noticeably shorter. The first upper row usually is sharply curved anteriorly in the midline (fig. 285A).

The dorsal part of the body is dark brown with a pale creamy gray, crescent-shaped mark on the posterior edge of the body. The venter is transparent with scattered brown flecks anterolaterally, especially below the eye. The caudal musculature is pale tan with a dark brown longitudinal streak on the middle of the anterior one-third of the tail, dark brown on the dorsal one-third of the tail, and brown flecks and blotches on the rest of the

musculature. The fins are transparent with brown flecks and blotches on the entire dorsal fin and posterior two-thirds of the ventral fin. The iris is bronze.

Duellman and Trueb (1966) noted that the coloration, especially the degree of pigmentation, is variable in the tadpoles of *Smilisca baudinii* and suggested that the intensity of pigmentation possibly is correlated with the amount of light. Tadpoles from sunlit pools were pallid by comparison with those from shaded forest pools. The authors also noted that the relative length and depth of the tail is variable but could not correlate this variation with geography.

**MATING CALL:** The call of *Smilisca baudinii* consists of a series of short, explosive notes, "wonk-wonk-wonk." Two to 15 notes comprise a call group; each note has a duration of 0.09 to 0.13 (mean, 0.11) seconds. Call groups are spaced from 15 seconds to several minutes apart. The notes have 140-195 (mean, 175), pulses per second and a fundamental frequency of 135 to 190 (mean, 166) cycles per second. Within the frequency spectrum two bands are emphasized; these major frequencies are at about 350 and 2500 cycles per second (pl. 32, fig. 1).

Duellman and Trueb (1966) pointed out the existence of an organization in the chorus structure in this species. This was elaborated upon by Duellman (1967a), who showed that *Smilisca baudinii* calls in duets; each chorus is made up of several pairs of calling males, and successive choruses apparently are initiated by the same duet.

Distress calls that are high pitched and emitted with the mouth open have been heard from both sexes of *Smilisca baudinii*.

**NATURAL HISTORY:** Throughout most of its range *Smilisca baudinii* inhabits xeric and subhumid regions having prolonged dry seasons. At unfavorable seasons this species takes refuge in bromeliads, in elephant-ear plants, in holes in trees, under bark of trees, and under the outer sheaths of banana plants. Throughout most of its range in México *Smilisca baudinii* is known to breed from June to October, but on the more humid Caribbean lowlands of Central America it apparently has a longer breeding season.

Although males call from nearly any body

of water, including cisterns and buckets, the usual breeding sites are shallow, temporary pools. Usually the males call from the ground at the edge of the water, but sometimes they sit in shallow water or perch on bushes and trees. Amplexus is axillary. The eggs are spread in a surface film on the water. Each deposition contains several hundred eggs having a diameter of about 1.3 mm. and encased in a vitelline membrane with a diameter of 1.5 mm. Duellman and Trueb (1966, p. 357) provided counts of 2620, 2940, and 3320 ovulated eggs removed from three female frogs.

Newly metamorphosed young have snout-vent lengths of 12.0 to 15.5 mm. (mean, 13.4 mm. in 23 specimens). The young usually are white below and dull olive-green above with faint brown transverse bands on the limbs. A white suborbital spot is a distinctive marking on the young of this species.

*Smilisca baudinii* is one of the most abundant and conspicuous (by its loud and distinctive call) of the Middle American hylids. Gadow (1908, p. 76) estimated 45,000 frogs at one breeding site in Veracruz, México, and I have encountered breeding congregations of several hundred, perhaps thousands, of individuals in México, Guatemala, and Costa Rica. Curiously, large numbers of *Smilisca baudinii* usually are not present at breeding ponds where numerous kinds of other frogs are calling. Instead, calling males of *S. baudinii* usually are at a separate pond. Exceptions do occur, and large choruses of *baudinii* have been found with *Phrynohyas venulosa*, *Tripurion spatulatus reticulatus*, *Rhinophrynus dorsalis*, *Engystomops pustulosus*, and *Bufo marmoratus*.

REMARKS: Duellman and Trueb (1966, p. 296) discussed the allocation of the various trivial names that are placed in the synonymy of *Smilisca baudinii*; the type specimens of all of the names proposed have been examined except *Hyla vociferans* Baird, for which no type was designated. Baird (1859, p. 35) designated figures 11-13 on plate 38 as *Hyla vociferans*; whether this was a lapsus for *Hyla vanvlietii*, which he described in 1854, or was intentionally the proposal of a new name cannot be ascertained. The figures quite clearly illustrate the frog now known as *Smilisca baudinii*. Duellman and Trueb (1966, p. 290)

erroneously regarded *Hyla vociferans* Baird as a *nomen nudum*. However, the rules of zoological nomenclature (Stoll, 1961, p. 11) clearly state that names based on an illustration, even though not accompanied by a description or designation of a specimen, prior to 1931, are to be regarded as valid. Thus, Duellman and Trueb's designation should be disregarded.

Barbour (1923) named *Hyla baudini dolomedes* from the Río Esnape, Darién Province, Panamá. Dunn (1931b) first pointed out that the holotype of *H. b. dolomedes* is a *Smilisca phaeota*.

The cranial osteology of *Smilisca baudinii* was described by Duellman and Trueb (1966) and by Trueb (1968b).

ETYMOLOGY: The specific name *baudinii* is a patronym for Monsieur Baudin, a French commander in México who donated the type specimen to the Museum National d'Histoire Naturelle in Paris.

DISTRIBUTION: *Smilisca baudinii* has a wide range throughout the lowlands (up to elevations of about 1000 meters) of Middle America from the Río Grande Embayment of Texas and southern Sonora, México, southward to Costa Rica, where on the Pacific lowlands the range terminates at the southern limits of the xeric scrub forest in the vicinity of Esparta; on the Caribbean lowlands the distribution apparently is discontinuous southward to Suretka (fig. 287). Stuart (1954c, p. 46) recorded the species at elevations up to 1400 meters in southeastern Guatemala, and Duellman and Trueb (1966, p. 298) gave 1600, 1675, and 1925 meters as the highest known elevations for the species in México.

See Appendix 1 for the locality records of the 3274 specimens examined.

#### *Smilisca eyanostieta* (Smith)

*Hyla phacota*: Smith and Taylor, 1948, p. 88.

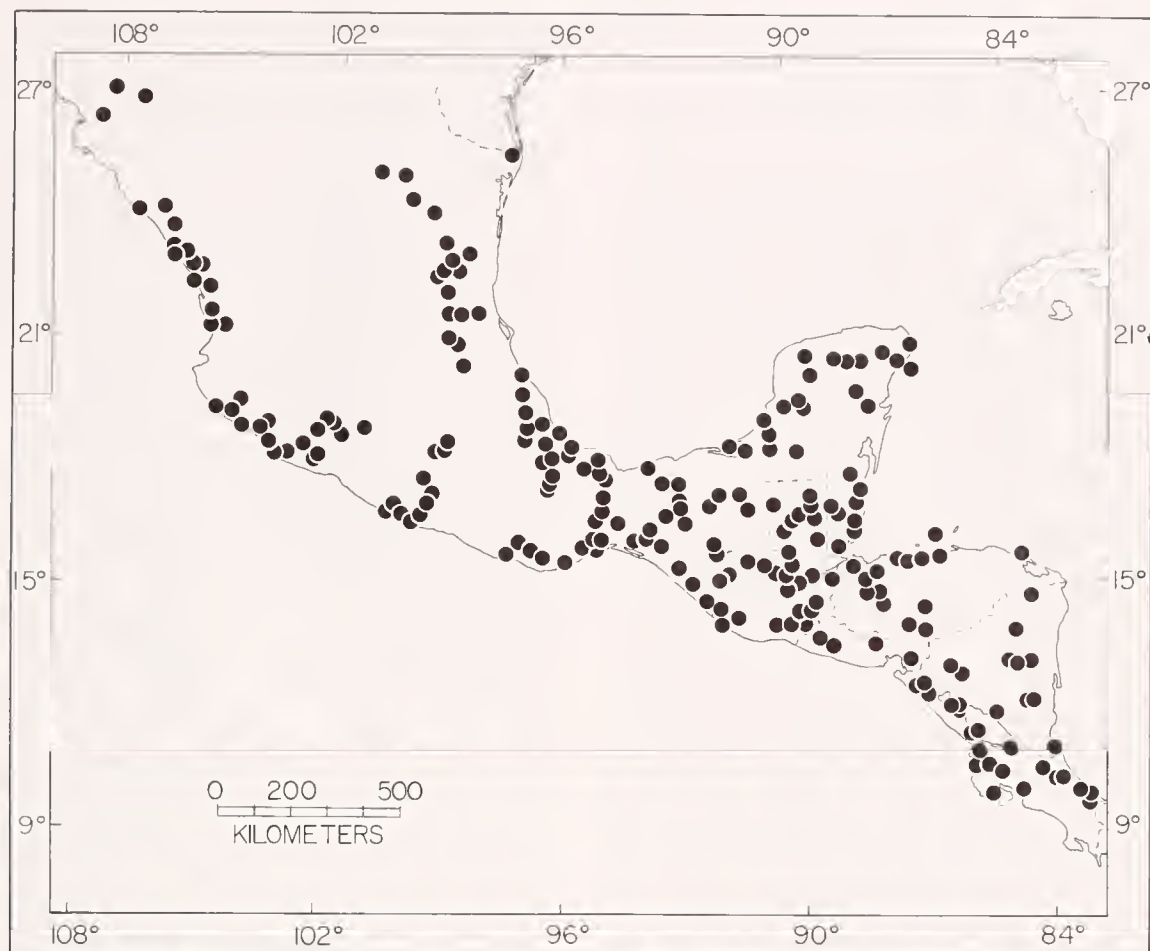
*Hyla phacota cyanostieta* Smith, 1953, p. 150 [holotype, U.S.N.M. No. 111147 from Piedras Negras, El Petén, Guatemala, elevation 100 meters; Hobart M. Smith collector].

*Smilisca phaeota* (*cyanostieta* by fiat): Starrett, 1960b, p. 303.

*Smilisca phacota cyanostieta*: Stuart, 1963, p. 42.

*Smilisca cyanostieta*: Duellman and Cole, 1965, p. 141. Duellman and Trueb, 1966, p. 303.



FIG. 287. Distribution of *Smilisca baudinii*.

**DIAGNOSIS:** This moderately large species of *Smilisca* has a low, flat, elliptical inner metatarsal tubercle, relatively long hind limbs (the ratio of tibia length to snout-vent length usually is greater than 0.520), and a sloping, moderately long snout. The presence of blue spots on the flanks and posterior surfaces of the thighs, a silvery white labial stripe, and a large brown postorbital mark distinguish *Smilisca cyanosticta* from all other Middle American hylids. *Smilisca sila* has blue spots on the flanks and thighs, but it has a short, truncate snout, smaller size (males, 45 mm.; females, 62 mm.), and lacks a white labial stripe and postorbital dark mark. *Smilisca phaeota* resembles *cyanosticta* in size, proportions, and coloration, except *phaeota* lacks blue spots. Faded specimens can be identified

by probing the lateral edge of the frontoparietals; large posterolaterally projecting supraorbital flanges are present in *phaeota*, whereas the flanges are narrow and not projecting in *cyanosticta*.

**DESCRIPTION:** Males of this moderately large species attain a maximum snout-vent length of 56 mm., and females reach 70 mm. The largest specimens are from Piedras Negras, El Petén, Guatemala; seven specimens have snout-vent lengths of 50.1 to 55.7 (mean, 52.5) mm. Specimens from the western part of the range are smaller; the snout-vent length varies from 46.6 to 56.8 (mean, 50.6) mm. in 10 specimens from Los Tuxtlas, Veracruz, and from 44.6 to 55.8 (mean, 50.3) mm. in 23 specimens from northern Oaxaca, México.

In a sample of 23 males from between

Yetla and Campamento Vista Hermosa, Oaxaca, México, the ratio of tibia length to snout-vent length is 0.519 to 0.597 (mean, 0.563); the ratio of head length to snout-vent length is 0.274 to 0.313 (mean, 0.294), and the ratio of the diameter of the tympanum to that of the eye is 0.644 to 0.788 (mean, 0.718). The average ratio of tibia length to snout-vent length is 0.564 in 10 males from Los Tuxtlas and 0.548 in seven males from Piedras Negras. In these same samples, respectively, the ratio of the diameter of the eye to that of the tympanum is 0.699 and 0.763. Thus, from west to east there is an increase in snout-vent length and relative size of the tympanum and a decrease in the relative length of the tibia. Females differ from males by having proportionately larger tympani; in four females the ratio of the diameter of the tympanum to that of the eye is 0.706 to 0.870 (mean, 0.783).

The head is about as wide as the body and is longer than wide; the top of the head is flat. The snout is long and slopes gradually from the eyes to the nostrils, which are about four-fifths the distance from the eyes to the tip of the snout. In lateral profile the snout is acutely rounded, and in dorsal profile it is bluntly rounded. The nostrils are noticeably protuberant. The canthus is round, but distinct; the loreal region is concave, and the lips are moderately thick and flared. A thin supratympanic fold extends from the posterior corner of the eye and curves over the upper edge of the tympanum to the insertion of the arm. The tympanum is distinct and separated from the eye by a distance equal to about one-half the diameter of the tympanum.

The arms are moderately long; no axillary membrane is present. A row of small tubercles is present on the ventrolateral edge of the forearm, and a distinct transverse fold is present on the wrist. The fingers are moderately short and broad. The discs are proportionately small; the width of the disc on the third finger is equal to about two-thirds the diameter of the tympanum. The subarticular tubercles are large and subconical; the distal tubercle on the fourth finger is flattened and slightly bifid in some specimens. The supernumerary tubercles are large, conical, and usually in one row on the proximal segments of the second, third, and fourth fingers. A

large, low, U-shaped outer palmar tubercle is divided into two elongate tubercles in some specimens. The prepollex is moderately enlarged and bears a horny nuptial exerescence in breeding males. The fingers are about one-third webbed (fig. 281B). A trace of web is present between the first and second fingers; the web extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are relatively long and slender; the adpressed heels overlap by about one-third the length of the shank, and the tibiotarsal articulation extends to a point between the eye and the tip of the snout. A thin transverse fold is present on the heel. The tarsal fold is thin and extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, and elliptical. The toes are moderately long and slender, and the discs are slightly smaller than those on the hands. The subarticular tubercles are small and round, and the supernumerary tubercles are small, subconical, and in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 282B). The web extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs and is covered by a short, broad anal sheath. The skin of the belly and posteroventral surfaces of the thighs is granular; the other surfaces are smooth. The tongue is ovoid, barely free behind, and shallowly notched anteriorly and posteriorly. There are four to 11 (mean, 7.1) prevomerine teeth situated on transverse ridges between the small oval choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is paired, subgular, and greatly distensible.

The general coloration of *Smilisca cyanostricta* is pale green or tan with olive-green or dark brown dorsal markings (pl. 70, fig. 3).

The dorsal markings usually consist of an interorbital mark, and a V-shaped mark in the occipital region with the anterior branches not extending to the eyelids. In many specimens this mark is continuous, by means of a narrow middorsal mark, with an inverted V-shaped mark in the scapular region. In some specimens these dorsal markings are fragmented into irregular spots, and in some specimens the dorsum is nearly uniform pale green or tan with a few small dark spots. Three or four dark transverse bands are present on the thigh and shank, and two or three bands are present on the tarsus. The webbing on the feet is brown. The loreal region is pale green. A dark brown canthal stripe extends from the nostril to the orbit and is bordered above by a narrow bronze-colored stripe, which continues along the edge of the eyelid to a point above the tympanum. The upper lip is silvery or creamy white, and the labial region below the eye is pale green. A broad dark brown mark, extending posteriorly from the eye to a point above the insertion of the arm, completely encompasses the tympanum. The flanks are dark brown with many pale blue, round spots, which give the impression of a pale blue ground color with dark brown mottling enclosing spots. The anterior and posterior surfaces of the thighs and the inner surfaces of the shanks and feet are dark brown with many small pale blue spots. Blue spots usually are present on the proximal segments of the second and third toes. A distinct white stripe is present on the outer edge of the tarsus and fifth toe and on the outer edge of the forearm and fourth finger. The anal region is dark brown and bordered above by a narrow transverse white stripe. The venter is creamy white; in breeding males the throat is dark grayish brown with white flecks. The iris is golden or bronze above and darker, usually brown, below. Small black flecks are present on the iris, and in some individuals the iris is so heavily flecked so as to appear gray.

Although no geographic variation occurs in the dorsal pattern, the pattern on the flanks is variable. Specimens from the eastern part of the range (Piedras Negras and Chinajá, Guatemala) have bold, dark reticulations on the flanks enclosing large pale blue or pale

green spots, which fade to tan in preservative. Specimens from Oaxaca and Vera Cruz, México, characteristically have finer dark reticulations and smaller blue spots on the flanks; in some of these specimens the ventrolateral spots are smallest and are white.

Living individuals have been observed to change from tan to brown, tan to green, pale green to tan, and pale green to dark green. Despite any metachrosis on the dorsum the labial region below the eye remains pale green, and the spots on the flanks and thighs are always present.

The ontogenetic change in coloration is striking and proceeds from pale tan flanks and orange yellow thighs, both lacking spots, to pale tan flanks and red thighs, both lacking spots, to dark brown flanks with blue spots and red thighs lacking spots, to dark brown flanks and thighs, both with blue spots. Juveniles have a pale tan dorsum with olive-green or dark brown markings; the white labial stripe is present.

**TADPOLES:** Ten hatchlings (developmental stage 21) have total lengths of 5.8 to 6.5 (mean, 6.28) mm.; 10 tadpoles in developmental stage 36 have total lengths of 27.0 to 30.0 (mean, 28.75) mm. The average ratio of tail length to total length in hatchlings is 0.521, and in stage 36 the ratio is 0.624.

A typical tadpole in developmental stage 30 has a total length of 25.0 mm. The body is slightly wider than deep; the snout is rounded laterally and broadly ovoid dorsally. The nostrils are about midway between the eyes and the tip of the snout. The spiracle is sinistral and slightly posterior to the mid-point of the body. The mouth is anteroventral, and the cloacal tube is dextral. The caudal musculature is slender, does not extend to the tip of the tail, and is barely curved upward distally. The dorsal fin does not extend onto the body and is slightly deeper than the ventral fin at midlength of the tail (fig. 284B).

The mouth is small and has well-developed lateral folds. The median part of the upper lip is bare, and the rest of the mouth is bordered by one row of bluntly rounded labial papillae, except that a few additional papillae are present in the lateral fold. The upper beak is moderately deep and forms a



broad arch with slender lateral processes. The lower beak is slender and broadly V-shaped; both beaks are finely serrate. There are two upper and three lower rows of teeth. All of the rows are about equal in length. The second upper row is broadly interrupted medially; the other rows are complete (fig. 285B).

The dorsal part of the body is dark brown; the ventral surfaces are transparent with greenish gold flecks, which disappear in preservative. The posterior edge of the body is cream in most specimens. The caudal musculature is gray in life and creamy white with interconnected brown spots in preservative. The caudal fins are transparent with small brown blotches on the dorsal fin and posterior half of the ventral fin. The iris is coppery bronze.

**MATING CALL:** The call of *Smilisca cyanosticta* consists of one or two moderately short notes, "wonk-wonk." Each note has a duration of 0.25 to 0.45 (mean, 0.38) seconds. Notes are repeated at intervals of about one-half minute to several minutes. The notes have 110 to 180 (mean, 147) pulses per second and a fundamental frequency of 135 to 160 (mean, 145) cycles per second. Two harmonies are emphasized, one at about 840 cycles per second and another at about 1900 cycles per second (pl. 32, fig. 2).

**NATURAL HISTORY:** *Smilisca cyanosticta* inhabits humid tropical and lower montane forests. In these moist environments the frogs apparently are active throughout most of the year. Males were calling in Oaxaca in June and July, in Veracruz in June, July, and August, and in Guatemala in March. Pyburn (1966, p. 2) stated that in Los Tuxtlas, Veracruz, breeding takes place in pools, in the forks of trees, depressions in logs, and in shallow pools. Duellman and Trueb (1966, p. 306) reported males calling from a water-filled depression in a log, in and near springs, in a quiet pool in a stream, and in a rain barrel. The latter authors thought that the eggs were deposited as loose clumps in the water, but Pyburn (1966) reported that the eggs are deposited as a thin surface film. Pyburn (1966, p. 6) stated that the eggs are 1.16 to 1.32 (mean, 1.22) mm. in diameter and are surrounded by a single envelope having a diameter of 1.68 to 2.04 (mean, 1.78) mm.

He stated that one captive female laid nine clutches of eggs between September 2, 1962, and October 13, 1963. Six of the clutches (the only ones counted) contained 437 to 1844 (mean, 1147) eggs. Duellman and Trueb (1966, p. 357) noted that one female contained 910 ovulated eggs.

Pyburn (1966) represented a description of the embryonic and larval development of this species; he found that tadpoles raised in the laboratory required 40 days after hatching to reach metamorphosis at a body length of about 14 mm., the same size given for recently metamorphosed young by Duellman and Trueb (1966, p. 307).

**REMARKS:** Smith (1953, p. 150) named *cyanosticta* as a subspecies of "*Hyla phaeota*." Superficially the two frogs have much in common, but as demonstrated by Duellman and Trueb (1966) the differences in cranial osteology and in the mating calls are highly suggestive of specific, rather than subspecific, differences. The most significant cranial differences are: the presence of a large fontoparietal fontanelle in *cyanosticta* and the absence of a fontanelle in *phaeota*, the presence of large posterolateral-projecting supra-orbital flanges in *phaeota* as compared with narrow non-projecting flanges in *cyanosticta*, and the attachment of the nasals to the sphenethmoid in *cyanosticta* and their separation in *phaeota*. The mating call of *cyanosticta* has a higher pulse rate and pitch than does that of *phaeota*. Furthermore, *phaeota* has only one low emphasized harmonic.

Pyburn (1966) discussed this species under the name *Hyla phaeota cyanosticta*.

**ETYMOLOGY:** The specific name *cyanosticta* is derived from the Greek *kyanos*, meaning dark blue, and *stiktos*, meaning spotted, and refers to the blue spots on the flanks and thighs.

**DISTRIBUTION:** *Smilisca cyanosticta* inhabits humid forests on the Atlantic slopes of southern México and northern Central America from northern Oaxaca and southern Veracruz through northern Chiapas in México and into El Petén and northern Alta Verapaz in Guatemala (fig. 288). The range is discontinuous; in southern México the species occurs in humid montane forests at elevations of 830 to 900 meters on the northern slopes of the

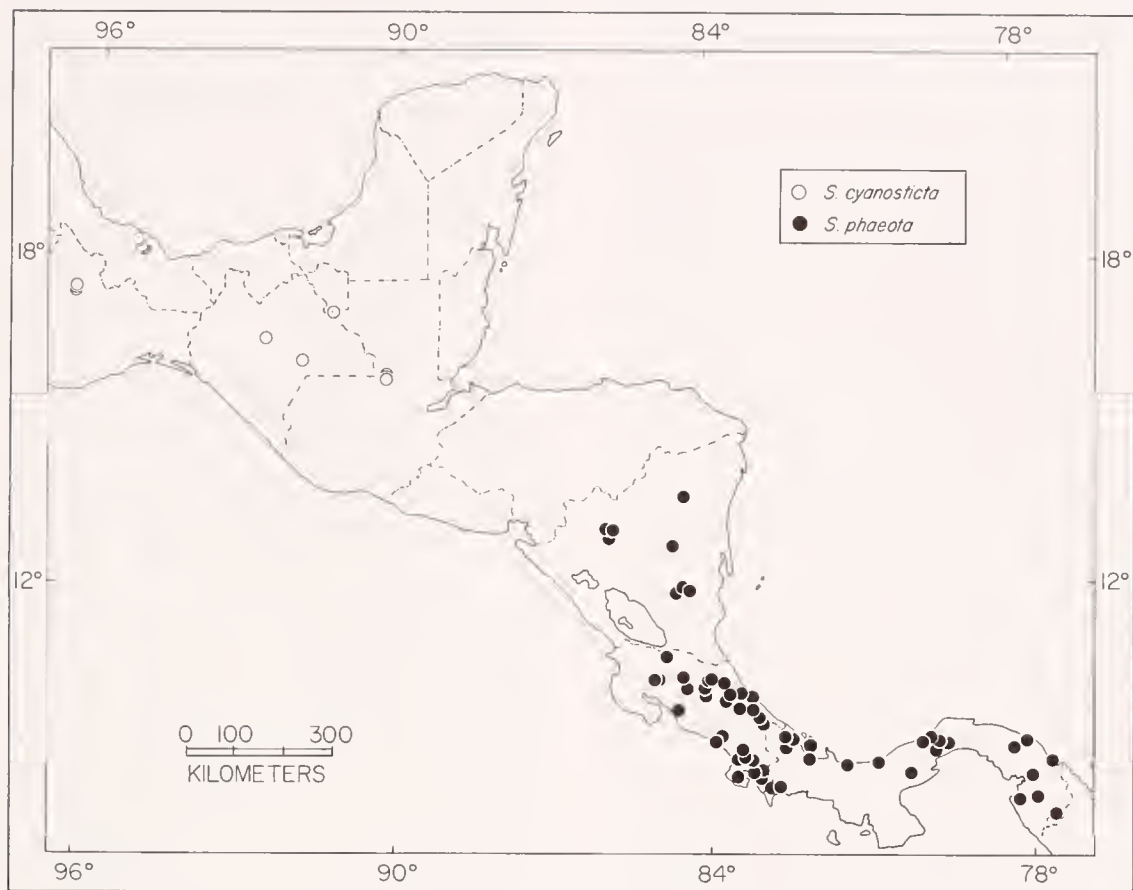


FIG. 288. Distribution of *Smilisca cyanosticta* and *Smilisca phaeota*.

Sierra de Juárez and at elevations of 300 to 1200 meters in the Sierra de los Tuxtlas, but it is absent in the intervening lowlands characterized by drier forest. The species is known from low elevations in the humid forests of El Petén and northern Alta Verapaz, Guatemala, but apparently is absent in the slightly drier forests in the northern part of the Isthmus of Tehuantepec.

In addition to the locality records of the 84 specimens examined listed in Appendix 1, Pyburn (1966) reported the species from three localities in the Sierra de Los Tuxtlas, Vera Cruz, México—2.7 kilometers south of Coyame, 5 kilometers east of Cuetzalapan, and 4 kilometers south-southwest of Sontecomapan.

#### *Smilisca phaeota* (Cope)

*Hyla phaeota* Cope, 1862, p. 358 [holotype, U.S.N.M. No. 4347 from Turbo, Intendencia de Chocó, Colombia, sea level; J. Cassin collector]. Boulenger, 1882a, p. 402. Günther, 1901 (1885-1902), p. 269. Taylor, 1952c, p. 837.

*Hyla baudini dolomedes* Barbour, 1923, p. 11 [holotype, M.C.Z. No. 8539 from Río Esnapé, Sambú Valley, Darién Province, Panamá; Thomas Barbour and Winthrop S. Brooks collectors].

*Hyla phaeota phaeota*: Smith, 1953, p. 152.

*Smilisca phaeota*: Starrett, 1960b, p. 303. Duellman and Trueb, 1966, p. 308.

**DIAGNOSIS:** This large species of *Smilisca* has a low, flat, elliptical inner metatarsal tubercle, relative long hind limbs (the ratio of tibia length to snout-vent length usually is greater than 0.520), and a sloping, moderately

long snout. The presence of a white labial stripe and a dark postorbital mark distinguishes *Smilisca phaeota* from all other Middle American hylids, except *S. cyanosticta*. The latter has blue spots on the flanks and on the anterior and posterior surfaces of the thighs, whereas in *phaeota* the flanks are pale green or tan with fine brown or black venation and the anterior and posterior surfaces of the thighs are pale brown with small cream spots on the posterior surfaces. *Smilisca baudinii* differs from *phaeota* by having a shorter, more truncate snout, dark, bold mottling on the flanks, and vertical bars on the upper lip.

DESCRIPTION: Males of this species attain a maximum snout-vent length of 65 mm.; females reach 78 mm. A considerable discrepancy in size occurs in different parts of the range. The average snout-vent length of 10 males from the Canal Zone is 56.5 mm., much the same as that in a sample from the Río Quesada, Chocó, Colombia (56.0 mm.). In equal samples of males from Puerto Viejo, Heredia, Costa Rica, and Bonanza, Zelaya, Nicaragua, the average snout-vent lengths are 51.7 mm. and 43.7 mm. respectively. The largest specimens are from the Golfo Dulce region in Puntarenas Province, Costa Rica, where the average snout-vent length is 61.4 mm. in 10 males.

In a sample of 10 males from the Atlantic side of the Canal Zone the ratio of tibia length to snout-vent length is 0.533 to 0.598 (mean, 0.578); the ratio of foot-length to snout-vent length is 0.400 to 0.458 (mean, 0.427); the ratio of head length to snout-vent length is 0.323 to 0.367 (mean, 0.349); the ratio of head width to snout-vent length is 0.335 to 0.376 (mean, 0.356), and the ratio of the diameter of the tympanum to that of the eye is 0.651 to 0.855 (mean, 0.749). In a sample of 10 females the only major difference in proportions is that the ratio of the diameter of the tympanum to that of the eye varies from 0.746 to 0.900 (mean, 0.805).

The head is about as wide as the body. The snout is moderately long and slopes gradually from the eyes to the nostrils, which are about four-fifths of the distance from the eyes to the tip of the snout. In lateral profile the snout is acutely rounded, and in dorsal profile it is bluntly rounded. The nostrils are

noticeably protuberant. The canthus is round, but distinct; the loreal region is concave, and the lips are moderately thick and flared. A moderately heavy supratympanic fold obscures the upper edge of the tympanum and curves downward to the insertion of the arm. The tympanum is distinct and separated from the eye by a distance equal to about one-half the diameter of the tympanum.

The arms are moderately long and slender. An axillary membrane is absent. A few small tubercles are present along the ventrolateral edge of the forearm in some specimens; a distinct transverse fold is present on the wrist. The fingers are moderately long and broad. The discs are relatively small; the width of the disc on the third finger is equal to about two-thirds the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercle on the fourth finger is bifid in some specimens. The supernumerary tubercles are large and conical. They are in one row on the proximal segment of each digit, except that in some specimens the tubercles are arranged in two irregular rows on the second digit. A flat, tripartite outer palmar tubercle is present. The prepollex is moderately enlarged and bears a horny nuptial excrescence in breeding males. The fingers are about one-third webbed (fig. 281C). A trace of web is present between the first and second fingers; the web extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The legs are relatively long and slender; the adpressed heels overlap by about one-third the length of the shank, and the tibiotarsal articulation extends to a point between the eye and the tip of the snout. A thin transverse dermal fold is present on the heel. The tarsal fold is thin and usually extends only about half the length of the tarsus. The inner metatarsal tubercle is low, flat, and elliptical. The toes are moderately long and slender; the discs are slightly smaller than those on the fingers. The subarticular tubercles are small and round; the supernumerary tubercles are small, subconical, and in a single row on each toe. The toes are about three-fourths webbed (fig. 282C). The web extends from the base



of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs and is covered by a short, broad anal sheath. The skin of the belly and posteroventral surfaces of the thighs is granular; the other surfaces are smooth. The tongue is a long ovoid, barely free behind, and not, or only shallowly notched posteriorly. There are five to nine (mean, 7.3) prevomerine teeth situated on transverse ridges between the small oval choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is paired, subgular, and greatly distensible.

The general coloration of *Smilisca phaeota* is pale green or tan with dark olive-green or dark brown dorsal markings (pl. 70, figs. 1 and 2). The dorsal markings usually consist of a dark interorbital mark and a broad blotch extending from the occiput to the sacral region. The dorsal blotch is irregular in shape; in some specimens it is fragmented into an anterior and a posterior blotch or into several spots. In most specimens the markings are bold, but in some the dorsal pattern is so faint as to be barely discernible. Four or five dark transverse bands are present on the thigh, five or six on the shank, and four on the tarsus. Usually two or three narrow bands are present on the proximal part of the fourth toe. The webbing on the feet is brown. The loreal region is pale green and is bordered above by a narrow dark brown canthal stripe extending from the nostril to the orbit. The upper lip is silvery white. A broad dark brown or black mark, extending posteriorly from the eye to a point above the insertion of the arm, completely encompasses the tympanum. The flanks are pale green to creamy tan and are marked with a fine dark brown or black venation. The anterior surfaces of the thighs are pale brown to grayish tan; in some specimens small darker flecks are present. The posterior surfaces of the thighs are similarly colored with dark flecks

present in most specimens and small cream-colored spots present in some individuals. A distinct white stripe is present on the outer edge of the forearm and fourth finger and on the outer edge of the tarsus and fifth toe; the latter stripe is bordered below by dark brown on the tarsus. The anal region is dark brown and usually bordered above by a narrow, transverse creamy white stripe. The venter is creamy white. In breeding males the throat is dark gray. The iris is bronze, darkest medially, and marked with fine black reticulations.

The only significant geographical variation in coloration is the presence of a faint tint of pale blue on the flanks in specimens from the Caribbean lowlands of Nicaragua and northeastern Costa Rica. Living individuals are capable of changing color from green to brown, or reverse.

Recently metamorphosed young usually are pale tan with brown on the sides of the head and on the flanks. The brown is separated from the dorsal color by a narrow cream stripe, which disappears when individuals reach a snout-vent length of about 20 mm. Also, at that stage of growth the dark pigment of the flanks dissipates into the finely venate pattern of the adults.

**TADPOLES:** Three hatchlings (developmental stage 21) have total lengths of 7.9 to 8.6 (mean, 8.21) mm. and an average ratio of tail length to total length of 0.477; in tadpoles in developmental stage 36 the ratio is 0.613. Tadpoles reach their maximum size at stage 39 when they have a body length of 14.0 mm. and a total length of as much as 39.8 mm. A detailed description of larval development was presented by Duellman and Trueb (1966).

A typical tadpole in developmental stage 30 has a total length of 22.9 mm. The body is as wide as deep; the snout is round in dorsal and lateral profiles. The nostrils are about midway between the eyes and the tip of the snout. The eyes are widely separated and directed dorsolaterally. The spiracle is sinistral and slightly ventral to the midline, and the spiracular opening is at about the midlength of the body. The mouth is anteroventral; the cloacal tube is short and dextral. The caudal musculature is slender, slightly curved

upward distally, and does not reach the tip of the tail. The dorsal fin extends onto the body and is deepest at about one-third of the length of the tail. At midlength of the tail the dorsal fin is slightly shallower than, or equal in depth to, the ventral fin (fig. 284C).

The mouth is moderately small and has well-developed lateral folds. The median part of the upper lip is bare; the rest of the mouth is bordered by one row of labial papillae. Additional papillae are present in the lateral fold. The upper beak is moderately deep and forms a broad arch with slender lateral processes. The lower beak is more slender and broadly V-shaped; both beaks have blunt serrations. There are two upper and three lower rows of teeth. The second upper row is slightly shorter than the first and broadly interrupted medially. The three lower rows are complete. The rows are about equal in length and slightly shorter than the second upper row (fig. 285C).

The dorsal part of the body is pale brown with a pale cream crescent-shaped mark on the posterior edge of the body. The belly is transparent with scattered brown flecks. The caudal musculature is pale creamy tan with brown spots. The fins are transparent with brown flecks and blotches. The iris is pale bronze.

**MATING CALL:** The call of *Smilisca phaeota* is a low vibrant growl. Each call group consists of one or two notes having a duration of 0.10 to 0.45 (mean, 0.31) seconds. Call groups are repeated at intervals of 20 seconds to several minutes. The notes have 100 to 130 (mean, 116) pulses per second and a fundamental frequency of 110 to 165 (mean, 143) cycles per second. Only one harmonic within the frequency spectrum is emphasized; this dominant frequency is at 330 to 495 (mean, 372) cycles per second (pl. 32, fig. 3).

**NATURAL HISTORY:** Throughout most of its range *Smilisca phaeota* inhabits humid lowland tropical forest. Because of rather equable climatic conditions, frogs of this species are active throughout the year. Although breeding activity is highest in the rainy season, slight showers in the drier parts of the year stimulate males to call. Males usually call from secluded spots at the edge of, or in, shallow temporary pools; occasionally indi-

viduals are found at the edges of streams or large ponds.

Duellman and Trueb (1966) reported that the eggs are deposited in loose clumps amidst vegetation. Subsequent observations indicate that probably the eggs are normally deposited in a surface film. Three females contained 1665, 1870, and 2010 ovulated eggs (Duellman and Trueb, 1966). Recently metamorphosed young have snout-vent lengths of 12.7 to 16.7 mm. (mean, 14.3 mm. in 11 specimens).

*Smilisca phaeota*, although not extremely abundant, is one of the frequently encountered hylids in lower Central America. Its habit of calling throughout the year in small temporary pools, often in the immediate vicinity of human habitation, make it one of the best known frogs to local people.

**REMARKS:** Dunn (1931b, p. 413) suggested that *Hyla baudinii dolomedes* Barbour (1923) from Darién Province, Panamá, was actually *Hyla phaeota*. Smith (1953) described *Hyla phaeota cyanosticta* from Piedras Negras, Guatemala. Duellman and Trueb (1966) concurred with Dunn's assignment of *dolomedes* but demonstrated that on the basis of cranial osteology and characteristics of the tadpoles and mating calls *cyanosticta* was not conspecific with *phaeota*.

Wilhelm Peters (1863, p. 463) named *Hyla labialis* from "umgegend von Bogota," Cundinamarca, Colombia, but in 1874 he regarded *Hyla labialis* to be identical with *Hyla phaeota* Cope, 1862. Günther Peters informed me that the holotype of *Hyla labialis* could not be found as of January 5, 1965, but that it was catalogued as number 4913 in the Zoologisches Museum Berlin. In the supposed absence of a type specimen of *Hyla labialis*, Duellman and Trueb (1966) followed Peters' decision in 1874 that his *Hyla labialis* was conspecific with *Hyla phaeota* Cope. In the summer of 1969 I found the type of *Hyla labialis* Peters in the Zoologisches Museum Berlin. The specimen (ZMB 4913) is not a *Smilisca phaeota*. The type specimen is the same as the Andean frogs subsequently named *Hyla wilsoniana* by Cope (1899).

**ETYMOLOGY:** The specific name *phaeota* apparently refers to the dark markings on the

dorsum and is derived from the Greek *phaios* meaning dark or dusky.

**DISTRIBUTION:** *Smilisca phaeota* is widely distributed below elevations of about 1000 meters in lower Central America (fig. 288). On the Caribbean lowlands it ranges from northeastern Nicaragua to northwestern Colombia and inland in the valleys of the Río Cauca and Río Magdalena; the species occurs on the Pacific lowlands from south-central Costa Rica to northwestern Ecuador, exclusive of the Panamanian savannas and the Azuero Peninsula.

See Appendix 1 for the locality records of the 581 specimens examined.

### *Smilisca puma* (Cope)

*Hyla puma* Cope, 1885b, p. 183 [holotype, U.S.N.M. No. 13735 from "Nicaragua"; J. F. Moser collector]. Günther, 1901 (1885-1902), p. 270.

*Hyla wellmanorum* Taylor, 1952c, p. 843 [holotype, K.U. No. 30302 from Batán, Limón Province, Costa Rica, elevation 15 meters; Edward H. Taylor collector].

*Smilisca wellmanorum*: Starrett, 1960b, p. 303.

*Smilisca puma*: Duellman and Trueb, 1966, p. 314.

**DIAGNOSIS:** This small species is easily distinguished from other members of the genus by the lack of webbing on the hand. The toes are about one-half webbed; the diameter of the tympanum is about two-thirds of that of the eye. A narrow white labial stripe is present. The dorsum is tan with a pair of dark brown (sometimes interconnected) longitudinal stripes on the back. The subarticular tubercles on the hand are relatively large, and the inner metatarsal tubercle is small. No other species of *Smilisca* has a pattern tending toward longitudinal stripes on the dorsum or has essentially no webbing in the hand.

**DESCRIPTION:** *Smilisca puma* is the smallest species in the genus; males attain a maximum snout-vent length of 38 mm., and females reach 46 mm. In a sample of 10 males from Puerto Viejo, Heredia Province, Costa Rica, the snout-vent length is 32.5 to 37.9 (mean, 34.8) mm. The ratio of the tibia to the snout-vent length is 0.484 to 0.529 (mean, 0.512); the ratio of foot length to snout-vent length is 0.375 to 0.426 (mean, 0.406); the ratio of the head length to the snout-vent length is 0.355 to 0.386 (mean, 0.373); the

ratio of the head width to the snout-vent length is 0.346 to 0.378 (mean, 0.361), and the ratio of the diameter of the tympanum to that of the eye is 0.521 to 0.718 (mean, 0.647).

The head is nearly as wide as the body and slightly narrower than wide. The top of the head is flat. In dorsal profile the snout is pointed; in lateral profile the snout is bluntly rounded. The snout is moderately long. The nostrils are noticeably protuberant and are situated at about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded but distinct; the loreal region is noticeably concave, and the lips are thin and moderately flared. A thin dermal fold extending posteriorly from the corner of the eye to a point above the insertion of the arm conceals the upper edge of the tympanum. The tympanum is otherwise distinct and separated from the eye by a distance about equal to the diameter of the tympanum.

The arm is moderately short; the upper arm is rather slender, and the forearm is noticeably robust. No axillary membrane is present. No distinct row of tubercles or dermal fold is present on the ventrolateral edge of the forearm, but a distinct transverse fold is present on the wrist. The fingers are short and stout and bear moderately large discs. The width of the disc on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are large and round; in a few individuals the distal tubercle on the fourth finger is slightly bifid. Supernumerary tubercles are absent except on the proximal part of the third and fourth fingers in some specimens; in these the tubercles are small and indistinct. The palmar tubercle is low, usually flat, and in most specimens rather indistinct. In some individuals the tubercle is bifid, tripartite, or fragmented into three or four small tubercles. The prepollex is barely enlarged, breeding males lack nuptial excrescences. Webbing is absent between the first and second fingers and vestigial between the others (fig. 281D). The hind limbs are moderately short and slender; the adpressed heels overlap by about one-fourth of the length of the shank, and the tibiotarsal articulation extends to the eye. A thin tarsal fold extends from between two-thirds to the full length of the tarsus. The inner metatarsal tubercle



is small, low, flat, and elliptical. The toes are moderately long and slender; the discs are about the same size as those on the fingers. The subarticular tubercles are moderately small and round; supernumerary tubercles are present only on the basal segments of the fourth and fifth digits. The toes are slightly more than one-half webbed (fig. 282D). The web connects the first and second toes at the bases of the penultimate phalanges; the web extends from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the antepenultimate of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs and is covered by a short anal sheath. The skin is granular on the belly and the posteroventral surfaces of the thighs; other surfaces are smooth. The tongue is cordiform, usually shallowly notched anteriorly and deeply notched posteriorly, and barely free behind. There are four to seven (mean, 5.3) provomerine teeth on high transverse ridges situated at a level between the posterior borders of the small round choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is paired, subgular, and greatly distensible.

The general coloration of *Smilisca puma* is yellowish-tan with brown markings on the dorsum (pl. 71, fig. 5). The markings on the back usually consist of a pair of dorsal stripes, variously modified. In some specimens the stripes are discreet and extend from the post-orbital region nearly to the vent, but in some specimens the stripes are connected by a transverse mark in the scapular region and in many others also by a transverse mark in the sacral region. In some specimens the stripes are fragmented posteriorly, and in one individual the dorsal pattern consists of two series of dark longitudinal dashes. Another specimen has two stripes fused middorsally for nearly their entire lengths. A dark brown interorbital mark is present; in most specimens this is in the form of an interorbital bar that extends onto the eyelids, but in some specimens the mark consists of a short V-

shaped mark or small spot between the eyes. There is no dark post-tympanic mark, but dark brown pigment forms a venated pattern from the axilla to the midflank. The inguinal region is white, finely mottled with dark brown. Some specimens have scattered metallic green flecks on the dorsum. The dorsal surfaces of the hind limbs are colored like the body and have two or three dark brown transverse marks on the thighs, three to five marks on the shanks, and one or two marks or irregularly arranged dark flecks on the tarsi. The posterior surfaces of the thighs are dark brown, and the webbing of the feet is tan to grayish brown. A narrow white stripe is present on the edge of the upper lip, and a transverse white stripe above the anus is invariably present. Narrow white stripes on the outer edges of the tarsi and of the forelimbs usually are distinct. The belly and ventral surfaces of the limbs are creamy white. In breeding males the vocal sac is grayish brown. The iris is a deep bronze.

**TADPOLES:** No recently hatched tadpoles or late developmental stages are available. Four tadpoles in developmental stage 34 have body lengths of 9.0 to 9.5 mm. and total lengths of 23.0 to 24.5 mm. The largest tadpole examined is in developmental stage 40 and has a total length of 31.0 mm. In a tadpole in developmental stage 34, the body is about three-fourths as deep as wide; the snout is round in dorsal and lateral profile. The nostrils are about midway between the eyes and the tip of the snout; the eyes are widely separated and directed dorsolaterally. The spiracle is sinistral and slightly ventral to the midline, and the spiracular opening is at about two-thirds of the length of the body. The mouth is anteroventral; the cloacal tube is short and dextral. The caudal musculature is slender and barely curved upward distally, and does not quite reach the tip of the tail. The dorsal fin extends onto the body and is deepest at about two-thirds of the length of the tail, where its depth is only slightly more than that of the ventral fin (fig. 284D).

The mouth is moderately small and has well-developed lateral folds. The median part of the upper lip is bare; the rest of the mouth is bordered by one or two rows of labial papillae plus additional papillae in the lateral

fold. The upper beak is shallow and forms a high arch with slender lateral processes. The lower beak is equally slender and broadly V-shaped; both beaks are finely serrate. There are two upper and three lower rows of teeth. The two upper rows are about equal in length, and the second row is broadly interrupted medially. The lower rows are complete. The first and second lower rows are about equal in length and nearly as long as the upper row, whereas the third lower row is noticeably shorter (fig. 285D).

The body is olive-brown with silvery green flecks laterally. The caudal musculature is olive-brown with greenish tan flecks. The fins are pale brown with greenish gold flecks. Dark reticulations are present on the caudal musculature and on the adjacent parts of the fins on the anterior half of the tail. The iris is deep bronze.

**MATING CALL:** The call of *Smilisca puma* consists of a low squawk, usually followed by a series of one or more rattling secondary notes. Call groups are spaced at intervals of five to 55 seconds. The duration of the primary notes varies from 0.06 to 0.35 (mean, 0.13) seconds, and that of the secondary notes is 0.10 to 0.47 seconds. The primary notes have 187 to 240 (mean, 208) pulses per second and have fundamental frequencies of 125 to 200 (mean, 145) cycles per second. Within the frequency spectrum two bands are emphasized; these major frequencies are at about 740 and 1870 cycles per second (pl. 33, fig. 1).

Duellman and Trueb (1966) noted that although individuals of *Smilisca puma* sometimes call alone, duets, trios, or quartets were more common. They observed that the chorus is initiated by one individual uttering primary notes until joined by a second, third, and fourth frog.

**NATURAL HISTORY:** *Smilisca puma* inhabits humid lowland tropical forest having more or less evenly distributed rainfall throughout the year. Except for periodic dry spells, frogs of this species seem to be active throughout most of the year. Calling males have been collected from February through September, and gravid females have been found in June, July, and August. Males call from shallow

water, where they are usually well hidden in the bases on dense clumps of grass.

One recently metamorphosed individual has a snout-vent length of 12.4 mm.

**REMARKS:** Comparison of the holotype of *Hyla wellmanorum* Taylor (K.U. No. 30302) with the holotype of *Hyla puma* Cope (U.S. N.M. No. 13735) leaves no doubt that both of these names apply to the same species. The type specimen of *puma* was part of a collection received at the United States National Museum from Lieutenant J. F. Moser from "Nicaragua." Duellman and Trueb (1966, p. 317) noted that on the basis of other species in the collection received from Moser, it is most likely that the holotype of *Smilisca puma* originated from the Caribbean lowlands of southeastern Nicaragua. However, to this date no specimens bearing specific locality have been received from Nicaragua, although the species is common in the Caribbean lowlands of Costa Rica.

Cochran (1961) listed *Hyla puma* Cope, as a synonym of *Hyla molitor* O. Schmidt, 1857. On the basis of Schmidt's description of *molitor* and a supposed syntype (N.M.W. No. 16494) it is inconceivable that *puma* and *molitor* are the same.

**ETYMOLOGY:** The specific name *puma* seemingly is an Indian name for a cat, from which is derived the vernacular name for *Felis concolor*. Possibly Cope used this name in elusion to the tawny dorsal color of the frog, which is not unlike that of the *puma*.

**DISTRIBUTION:** This species lives in the wet, forested region of the Caribbean lowlands of Costa Rica and presumably southern Nicaragua (fig. 289). All specimens are from low elevations; the highest record of occurrence of this frog is 285 meters at Laguna Bonilla.

See Appendix 1 for the locality records of the 65 specimens examined.

#### *Smilisca sila* Duellman and Trueb

*Smilisca sila* Duellman and Trueb, 1966, p. 318 [holotype, K.U. No. 91852 from El Volcán, Chiriquí Province, Panamá, elevation 1280 meters; William E. Duellman collector].

**DIAGNOSIS:** This moderate-sized member of the genus differs from all other species by having a short truncate snout and in lacking

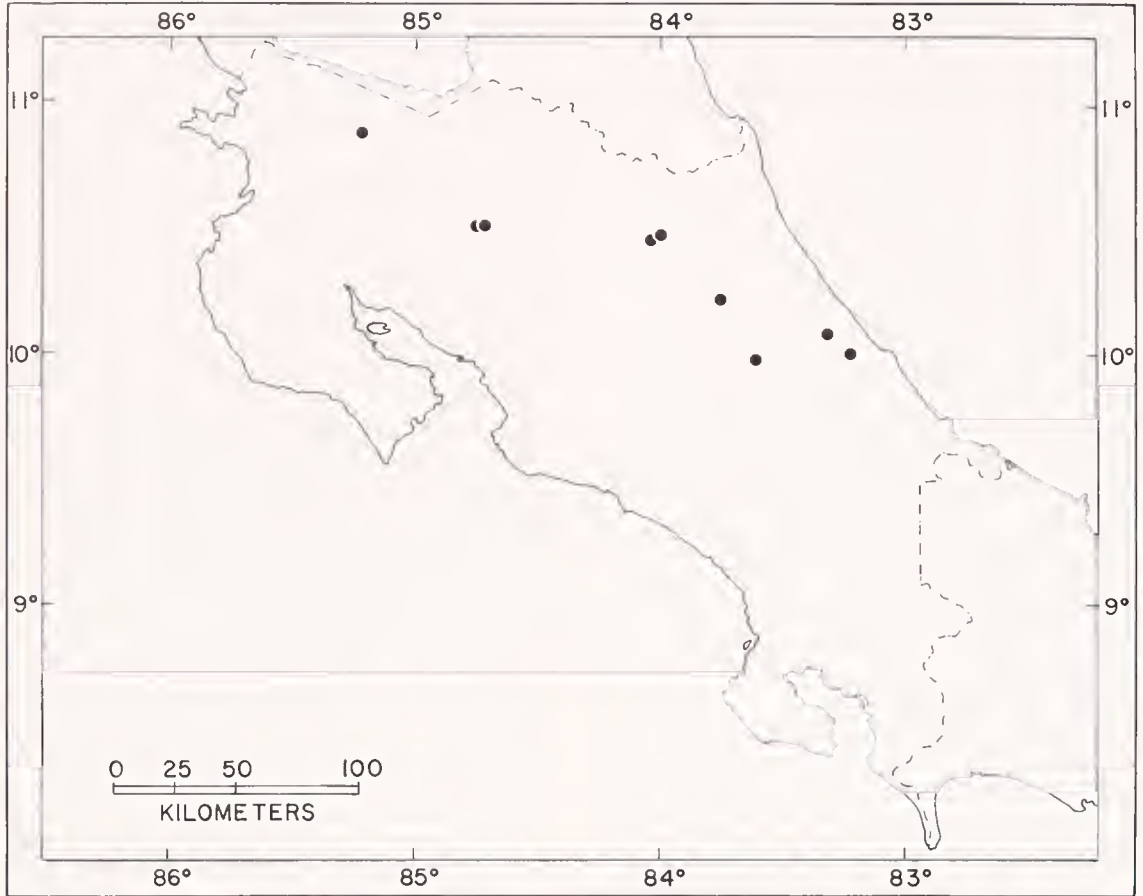


FIG. 289. Distribution of *Smilisca puma*.

a dark brown or black postorbital mark. The lips are thick and rounded, and the diameter of the tympanum is about one-half that of the eye. The margin of the upper lip is faintly marked by an interrupted white stripe. The flanks and posterior surfaces of the thighs are dark brown or black with pale blue to creamy tan spots or flecks. Blue spots are present on the flanks of *S. cyanosticta* and some *S. sordida*. The former is a larger (males to 56 mm.; females to 70 mm.) species having a longer, more sloping snout, and a dark brown postorbital mark. The snout is low and sloping in *S. sordida*. The lips are thin and flaring, and the throat in breeding males is white, whereas the throat in *sila* is dark brown. *Smilisca baudinii* is the only other genus having a moderately short and truncate snout, but this species is large (males to 76 mm.; females to 90 mm.); furthermore,

*baudinii* has a dark postorbital mark and has creamy yellow flanks with black or brown mottling.

DESCRIPTION: *Smilisca sila* is a moderate-sized species of the genus; males attain a maximum snout-vent length of 45 mm., and females reach 62 mm. In a sample of 10 males from Finca La Sumbadora, Panamá Province, Panamá, the snout-vent length is 40.0 to 44.8 (mean, 42.3) mm. The ratio of the tibia length to the snout-vent length is 0.511 to 0.568 (mean, 0.540); the ratio of the foot length to snout-vent length is 0.376 to 0.439 (mean, 0.411); the ratio of head length to snout-vent length is 0.326 to 0.356 (mean, 0.344); the ratio of head width to snout-vent length is 0.337 to 0.368 (mean, 0.352), and the ratio of the diameter of the tympanum to that of the eye is 0.481 to 0.580 (mean, 0.532).

There is a geographic gradient in size;



specimens from the western part of the range (southern Costa Rica) are smaller than those in the eastern part of the range (eastern Panamá). Five males from the Pacific lowlands of southern Costa Rica have snout-vent lengths of 31.6 to 38.2 (mean, 34.7) mm.; 10 males from El Volcán, Chiriquí Province, Panamá, have snout-vent lengths of 32.6 to 37.9 (mean, 36.4) mm., and eight males from Barro Colorado Island, Canal Zone, have snout-vent lengths of 38.2 to 42.0 (mean, 35.6) mm. These are smaller than the males from Finca La Sumbadora, which is east of the Canal Zone. Ten females from El Volcán have snout-vent lengths of 44.2 to 55.6 (mean, 49.2) mm., as compared with 56.1 to 62.2 (mean, 58.2) mm. in three females from Finca La Sumbadora.

The head is about as long as broad and is as broad as the body. The top of the head is flat. In dorsal and lateral profiles the snout is truncate. The snout is extremely short. The diameter of the eye is nearly equal to the distance from the anterior corner of the eye to the tip of the snout. The nostrils are moderately protuberant and are situated at about three-fourths the distance from the anterior corner of the eye to the tip of the snout. The canthus is angular; the loreal region is slightly concave, and the lips are thick and barely flared. A moderately heavy dermal fold extends posteriorly from the posterior corner of the eye, above the tympanum, and curves downward to the place of insertion of the arm. The upper edge of the tympanum is concealed beneath the dermal fold. Otherwise the tympanum is distinct and separated from the eye by a distance about equal to the diameter of the tympanum.

The arm is rather short; the upper arm is slender, and the forearm is moderately robust. No axillary membrane is present. A row of low, indistinct tubercles is present on the ventrolateral edge of the forearm, and an indistinct transverse fold is present on the wrist. The fingers are moderately long and stout and bear rather small discs. The width of the disc on the third finger is about two-thirds of the diameter of the tympanum. The subarticular tubercles are moderately large and conical; none is bifid. The supernumerary tubercles are small and indistinct; they are present

only on the proximal segments of the second, third, and fourth fingers. A flat, indistinct, triangular shaped palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about half webbed (fig. 283A). A trace of web exists between the first and second fingers. The web extends from the middle of the penultimate phalanx of the second finger to the proximal end of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the adpressed heels overlap by about one-fourth of the length of the shank, and the tibiotarsal articulation extends to a point between the eye and the nostril. The tarsal fold is thin and flap-like, and extends the entire length of the tarsus. The inner metatarsal tubercle is low, flat, and elliptical. The toes are moderately long and slender; the discs are slightly smaller than those on the fingers. The subarticular tubercles are large and subconical; the supernumerary tubercles are moderately large, conical, and in a single row on the proximal segment of each toe. The toes are about four-fifths webbed (fig. 283C). The web extends from the base of the disc of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, and from the base of the disc of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs and is covered by a short anal sheath. Large females from throughout the range and some males from Costa Rica and western Panamá have scattered small tubercles on the head and back. In other specimens, the dorsal surfaces are smooth. The belly and posteroventral surfaces of the thighs are granular. The tongue is broadly cordiform, very shallowly notched posteriorly, and barely free behind. There are five to seven (mean, 5.7) prevomerine teeth on high, rounded, transverse ridges between the posterior margins of the small, ovoid inner nares. The vocal slits

extend from the midlateral base of the tongue to the angle of the jaws. The vocal sac is paired, subgular, and greatly distensible.

The general coloration of *Smilisca sila* consists of a gray, tan, or pale reddish brown dorsal ground color and a creamy white venter. The dorsum is marked by dark brown, olive-brown, or dark reddish brown spots or blotches (pl. 71, figs. 3 and 4). Usually the blotches are discrete, but in some individuals they are interconnected and form an irregular dark mark on the dorsum. There is no tendency for the blotches to form transverse bars as in some *Smilisca sordida*. In some females the dorsal markings are reduced to a few small spots or are nearly absent, whereas in other females the dorsal markings are bold. White, pustular spots or metallic green flecks are present on the dorsal surfaces of many individuals. The dorsal surfaces of the limbs are colored like the body with dark brown transverse bars; usually three or four bars are present on each forearm, thigh, and shank, usually the flanks and posterior surfaces of the thighs have black mottling enclosing pale blue spots and flecks respectively, but the coloration of the flanks and limbs varies geographically.

Specimens from southern Costa Rica and western Panamá have distinct bars on the limbs; the posterior surfaces of the thighs have brown reticulations enclosing small blue flecks in specimens from Costa Rica and bolder, black reticulations enclosing large pale blue spots in specimens from western Panamá. In specimens from Costa Rica the flanks are brown with pale blue flecks, whereas those from Chiriquí, Panamá, the flanks are pale blue with dark brown mottling in the inguinal region. Frogs from El Valle and Cerro La Campana usually have distinct bars on the limbs; the posterior surfaces of the thighs are colored as in frogs from Chiriquí, and the inguinal region is pale blue with coarse brown mottling. Specimens from Barro Colorado Island, are marked like those from El Valle and Cerro La Campana, except that on the posterior surfaces the thighs fine black reticulations enclosed many pale blue spots. In specimens from Darién and Panamá provinces, east of the Canal Zone (Altos de Pacora, Cerro Jefe, Finca La Sumbadora, and

Río Pacora), the markings on the dorsal surfaces of the limbs are indistinct or absent in males, but distinct in some females. Intense brown and black pigment forms fine reticulations delimiting bold blue spots on the flanks. This coloration extends to the axilla in many specimens. Fine black reticulations enclose many dark blue spots on the posterior surfaces of the thighs. In living individuals from Costa Rica and western Panamá the blue coloration on the flanks and thighs is much less conspicuous than in specimens from eastern Panamá. In females the throat is creamy white; in some specimens scattered brown flecks are present on the chin and throat. In breeding males the anterior part of the throat is dark gray or dark brown. The color of the iris is variable, even in frogs from one locality. The color varies from pale brown to grayish brown with or without a metallic bronze suffusion and dark brown or black reticulations.

The labial region is usually indistinctly marked by dark vertical bars separated by paler ground color. The edge of the upper lip is marked by a creamy white stripe which is broadly interrupted by the vertical dark bars. In many specimens the labial stripe is nearly indistinguishable.

A recently metamorphosed young had, in life, a brown dorsum with darker brown markings, a white spot below the eye and a narrow white labial stripe. The belly was white; the flanks were brown with white spots and the posterior surfaces of the thighs were yellowish tan.

**TADPOLES:** Eleven tadpoles in developmental stage 25 have total lengths of 25.9 to 31.0 (mean, 28.1) mm.; one tadpole in stage 42 has a total length of 42.0 mm. A typical tadpole in developmental stage 25 has a total length of 28.5 mm. The body is only slightly wider than deep and nearly flat dorsally; the snout is broadly rounded in dorsal view and bluntly rounded in lateral view. The nostrils are slightly closer to the eyes than to the tip of the snout. The eyes are widely separated and directed dorsolaterally. The mouth is ventral; the eloaduct tube is short and dextral. The spiracle is sinistral and slightly ventral to the midline, and the spiracular opening is at about two-thirds of the distance from the snout to the posterior edge of the body. The

caudal musculature is moderately heavy and straight; the musculature extends to the tip of the tail. The dorsal fin extends onto the body; the fins are deepest at about two-fifths of the length of the tail, where the depth of the caudal musculature is about equal to the depth of the dorsal and the depth of the ventral fin (fig. 284E).

The mouth is moderately large and has extensive lateral folds. The median part of the upper lip is bare; the rest of the upper lip is bordered by one row of labial papillae; and the lower lip is bordered by one or two rows of labial papillae. Many small papillae are present in the lateral folds. The upper beak is moderately massive, and its inner surface forms a continuous arch with the short lateral processes. The lower beak is less robust and is broadly V-shaped; both beaks bear blunt serrations. There are two upper and three lower rows of teeth. The upper rows are about equal in length and broadly V-shaped. The second upper row is narrowly interrupted medially. The lower rows are complete and about equal in length, but slightly shorter than the upper rows (fig. 285E).

In preservative the dorsal part of the body is dark grayish brown with dark brown spots dorsally and white flecks laterally; the venter is pale grayish tan. The caudal musculature is pale tan with brown flecks over the entire surface and dark brown streaks on the posterior half of the ventral fin and on all of the dorsal fin.

**MATING CALL:** The call of *Smilisca sila* consists of a low squawk, usually followed by a series of one or more rattling secondary notes. Call groups are repeated at intervals of four to 20 seconds. The duration of the primary notes is 0.06 to 0.28 (mean, 0.16) seconds, and of the secondary notes, 0.14 to 0.48 seconds. The primary notes have 97 to 120 (mean, 108) pulses per second and a fundamental frequency of 90 to 115 (mean, 103) cycles per second. Two bands are emphasized within the frequency spectrum; these major frequencies are at about 900 and 2200 cycles per second (pl. 33, fig. 2).

**NATURAL HISTORY:** *Smilisca sila* is an inhabitant of shallow rocky streams. The breeding season seems to be correlated with the

time of the year when the water is clear and at a low level; consequently, the major breeding activity takes place in the dry season. Males call from the edges of small, shallow streams, from rocks in the stream or less frequently from vegetation overhanging the streams. Females are most frequently found on the banks of streams, and clasping pairs are usually in shallow pools in streams. Tadpoles have been found in pools in clear streams; some tadpoles have been observed to cling by their mouths to rocks in the streams; others were found on the bottom where they seek refuge among the pebbles or under rocks or leaves.

Metamorphosing young have been found on vegetation at the edges of streams and have been raised at the laboratory. Seven recently metamorphosed young have snout-vent lengths of 13.6 and 15.6 (mean, 14.6) mm.

**REMARKS:** Duellman and Trueb (1966) demonstrated that this species is distinct from *Smilisca sordida*; both species had been confused under the name of *Hyla* (*Smilisca*) *gabbi*. With the exception of the type description of *Smilisca sordida*, all references to "*Hyla sordida*" and "*Hyla gabbi*" in Panamá are based on *Smilisca sila*.

**ETYMOLOGY:** The specific name *sila* refers to the blunt snout and is derived from the Latin *silus* meaning "pug-nosed."

**DISTRIBUTION:** *Smilisca sila* ranges along the Pacific slopes and lowlands of Costa Rica and Panamá at elevations from sea level to about 1300 meters; in eastern Panamá and northern South America the species occurs on the Caribbean slopes and in the valleys of the northward draining rivers of Colombia (fig. 290).

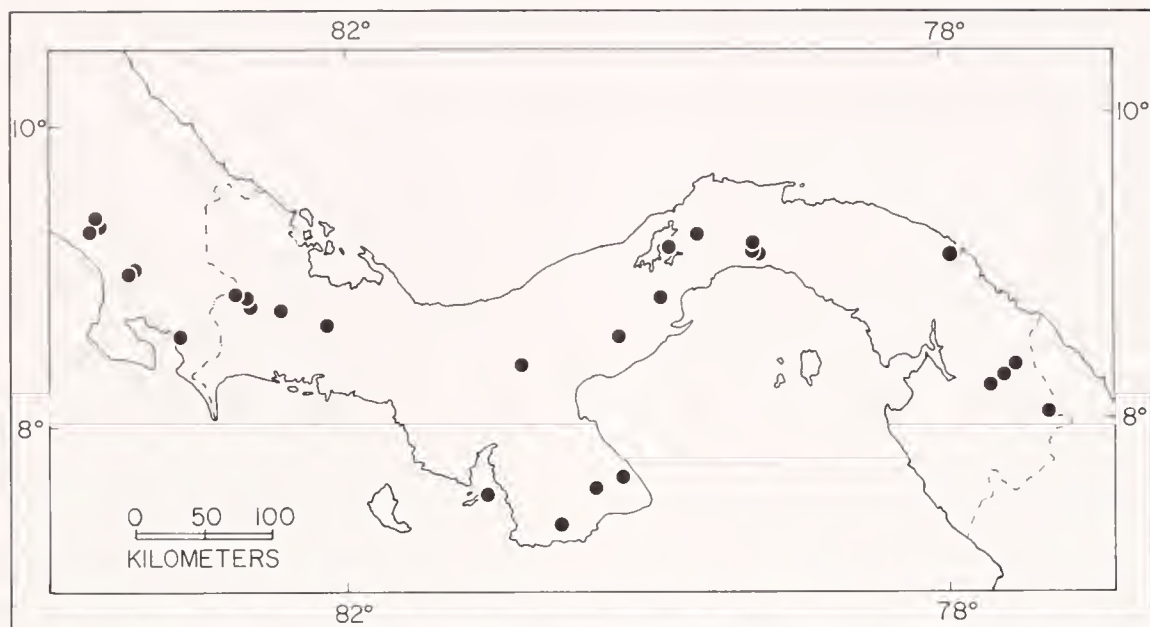
See Appendix 1 for the locality records of the 270 specimens examined.

### *Smilisca sordida* (Peters)

*Hyla sordida* Peters, 1863, p. 460 [syntypes, Z.M.B. 3141 (2 specimens) from "Veraguas," Panamá; J. von Warzewicz collector]. Brocchi, 1882, p. 42. Boulenger, 1882a, p. 393. Günther, 1901 (1885-1902), p. 273.

*Hyla gabbi* Cope, 1876, p. 103 [syntypes, U.S.N.M. Nos. 30658 and 30659 from "near Sipurio," Limón Province, Costa Rica, elevation 60 meters; William M.



FIG. 290. Distribution of *Smilisca sila*.

Gabb collector]. Brocchi, 1882, p. 37. Boulenger, 1882a, p. 372. Cünther, 1901 (1885-1902), p. 274. Taylor, 1952c, p. 840.

*Hyla nigripes* Cope, 1876, p. 104 [syntypes, U.S.N.M. Nos. 30685 and 30686 from "Pico Blanco," Limón Province, Costa Rica; William M. Gabb collector]. Brocchi, 1882, p. 38. Boulenger, 1882a, p. 394. Cünther 1901 (1885-1902), p. 278. Taylor, 1952c, p. 853.

*Hyla salvini* Boulenger, 1882a, p. 372 [syntypes B.M.N.H. No. 1947.2.24.12 from Costa Rica; Osbert Salvin collector; B.M.N.H. No. and 1947.2.24.13 from Cartago Province, Costa Rica, elevation 1470 meters; Jansen collector].

*Smilisca gabbi*: Starrett, 1960b, p. 303.

*Smilisca sordida*: Duellman and Trueb, 1966, p. 323.

**DIAGNOSIS:** This moderate-sized member of the genus is distinguished from the other species by the presence of a white vocal sac in breeding males. The diameter of the tympanum is about one-half that of the eye, and the lips are thin and flaring. The inner metatarsal tubercle is long, low, flat, and elliptical. The fingers are about one-half webbed; the toes are four-fifths webbed. The dorsum is variously marked with dark gray, dark brown, reddish-brown, or olive-green spots or blotches. The flanks and posterior surfaces of the thighs are dark brown with bluish white and

creamy tan flecks respectively. There is no white labial stripe. Blue spots are present on the flanks of *S. cyanosticta* and *sila*. The former is a larger species (males to 56 mm.; females to 70 mm.) having a white labial stripe and a large dark brown postorbital mark. In *S. sila* the snout is short and truncate, the lips are thick and not flaring, and the throat in breeding males is dark gray or brown.

**DESCRIPTION:** Males of *Smilisca sordida* attain a maximum snout-vent length of 45 mm., and females, 64 mm. In a sample of 10 adult males from 15 to 20 kilometers west-southwest of San Isidro el General, San José Province, Costa Rica, the snout-vent length is 38.1 to 42.6 (mean, 40.5) mm.; the ratio of tibia length to snout-vent length is 0.505 to 0.538 (mean, 0.523); the ratio of foot length to snout-vent length is 0.406 to 0.440 (mean, 0.426); the ratio of head length to snout-vent length is 0.329 to 0.351 (mean, 0.343); the ratio of head width to snout-vent length is 0.291 to 0.322 (mean, 0.313), and the ratio of the diameter of the tympanum to that of the eye is 0.449 to 0.571 (mean, 0.489). Specimens from the Pacific slopes of Costa Rica are larger than those from the Meseta Central

TABLE 58

Comparison of Snout-vent Lengths, with Means in Parentheses, in six Samples of Males of *Smilisca sordida* from Costa Rica.

Locality	N	Snout-vent Length
Puntarenas:		
Golfito .....	10	38.4-44.6 (41.8)
Puntarenas:		
Rincón de Osa .....	20	38.3-42.1 (40.8)
San José:		
San Isidro el General	10	38.1-42.6 (40.5)
San José:		
Eseazú and Río Joreo	10	34.3-37.6 (36.0)
Alajuela:		
La Fortuna .....	10	31.9-36.0 (34.4)
Limón:		
Pandora .....	10	33.8-37.6 (35.9)

and from the Caribbean lowlands (table 58). The only noticeable differences in proportions between males and females is in the ratio of the tympanum to that of the eye; for example, the mean ratio in 10 males from the Meseta Central is 0.493 and in eight females, is 0.614.

The head is about as wide as the body and slightly longer than wide. The top of the head is flat. In dorsal profile the snout is acutely rounded. In lateral profile the shape of the snout varies geographically and sexually. Specimens from the Caribbean lowlands have blunt snouts; those from the Pacific lowlands have longer, more slender snouts that are pointed in lateral view, and those from the Meseta Central are intermediate in snout shape between the two lowland populations. These differences in the shape of the snout are dependent on the nature of the underlying cranial bones, principally the maxillary and nasals. In specimens from the Caribbean lowlands, the nasals are long, wide, and barely separated from the sphenethmoid; the anterior edge is just posterior to the nostril. The maxillary flanges are nearly vertical. In specimens from the Pacific lowlands the nasals are relatively shorter, narrower, and rather widely separated from the sphenethmoid; the anterior edges of the nasals do not extend so far forward as the specimens from the Caribbean lowlands. The maxillary phalanges slant medially. In

these cranial characters, specimens from the Meseta Central are intermediate between the two lowland populations. Superimposed on this geographic variation are ontogenetic changes, which are most noticeable in males. In smaller, and presumably younger, specimens the snouts are more pointed than in larger specimens; consequently, some small males from the Caribbean lowlands resemble larger males from the Pacific lowlands, since the nasals and maxillaries of the former are not fully ossified. In addition, in small breeding males the sphenethmoid is only about one-half ossified, a large frontoparietal fontanelle is present, the anterior arm of the squamosal extends only about one-fourth the distance to the maxillary (two-thirds the distance in larger specimens), and the prootics are short, as compared with the long, thin elements in larger specimens. The nostrils are slightly protuberant and are situated at about three-fourths of the distance from the eyes to the tip of the snout. The canthus is slightly angular; the loreal region is noticeably concave, and the lips are thin and flaring. A moderately heavy dermal fold extends posteriorly from the posterior corner of the eye to a point above the insertion of the arm; the fold obscures the upper edge of the tympanum, which is otherwise distinct and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arm is moderately long; the upper arm is slender, and the forearm is somewhat more robust. A distinct axillary membrane is absent. A row of low tubercles forms a scalloped dermal ridge along the ventrolateral edge of the forearm, and a faint transverse fold is present on the wrist. The fingers are rather short and stout and bear large discs. The width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercle on the fourth finger is flattened and in about one-third of the specimens is bifid. The supernumerary tubercles are moderately small, conical, and usually present in a single row on the proximal segments of each digit. No distinct palmar tubercle is present, although a cluster of small tubercles sometimes is fused on the palm. The prepollex is noticeably enlarged and in

breeding males bears an extensive horny nuptial excrecence. The fingers are about one-half webbed (fig. 283B). The webbing is vestigial between the first and second fingers, and extends from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, and from the base of the penultimate phalanx of the third to the distal end of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and slender; the adpressed heels overlap by about one-fourth of the length of the shank, and the tibiotarsal articulation extends to a point between the eye and the tip of the snout. The tarsal fold is thin and extends the full length of the tarsus. The inner metatarsal tubercle is long, low, flat and elliptical. The toes are long and relatively slender; the discs are slightly smaller than those on the fingers. The subarticular tubercles are moderately large, round, and subconical; the supernumerary tubercles are small, conical, and widely dispersed in a single row on the proximal segments of each toe. The toes are about four-fifths webbed (fig. 283D). The web connects the first and second toes at the bases of the discs; the web extends from the base of the disc of the second toe to the middle of the penultimate phalanx of the third, from the base of the disc of the third to the middle of the penultimate phalanx of the fourth and on to the disc of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs and is covered by a short anal sheath. The skin is granular on the belly and the posteroventral surfaces of the thighs; the other surfaces are smooth. The tongue is broadly eordiform, usually shallowly notched anteriorly and posteriorly, and barely free behind. There are four to six (mean, 5.2) prevomerine teeth on small transverse ridges between the ovoid choanae. The vocal slit extends from the midlateral base of the tongue to the angles of the jaws. The vocal sac is bilobate and not greatly distensible.

The dorsal ground color of *Smilisca sordida* is gray, pale tan, or reddish brown; the venter is white. The dorsum is variously marked with dark gray, dark brown, reddish brown, or olive-green spots or blotches (pl.

71, figs. 1 and 2). The limbs are banded with dark brown, or olive-green. The flanks are dark brown with cream, greenish gray, or bluish gray mottling. The posterior surfaces of the thighs are dark brown with pale blue, pale green, or tan flecks. The iris varies from creamy silver to grayish yellow or bronze with a variable amount of black reticulations.

A dark interorbital bar usually is present. Dorsal markings on the body usually consist of a blotch, or two or more spots, on the occiput, in the scapular region, and in the sacral region. In many specimens, especially females, these markings are in the form of broad transverse bars. A few individuals lack dorsal markings or have scattered dark flecks on the back. Some individuals have scattered small white spots on the dorsum. White labial stripes and anal stripes are absent in all specimens. The transverse bars on the limbs are indistinct in some specimens from the Meseta Central and the Caribbean lowlands, whereas the bands are distinct in all specimens from the Pacific lowlands. Specimens from the Caribbean lowlands have two to six bars on each shank, whereas specimens from the Pacific slopes have four to six bars on the shank, and specimens from the Meseta Central has as many as eight bars on each shank. The flanks and the posterior surfaces of the thighs are usually marked by bluish white or creamy tan flecks, respectively, but this coloration varies considerably. In specimens from the Caribbean lowlands a small amount of flecking is present in the inguinal region; on the posterior surfaces of the thighs flecks are few or absent. In specimens from the Meseta Central, numerous large flecks or small round spots (pale bluish white in life) are present on the posterior half of the flanks; small flecks are present on the posterior surfaces of the thighs. Specimens from the Pacific slopes and the lowlands of southern Costa Rica (Puntarenas and San José provinces) have bold mottling of black and bluish white on the flanks and many bluish white flecks on the posterior surfaces of the thighs. In specimens from the Pacific slopes of Guanacaste in northwestern Costa Rica, flecks are present in the inguinal region; indistinct flecks are present on the posterior surfaces of the thighs. The throat is immaculate in



specimens from the Caribbean lowlands in Limón Province; the throats are dusky laterally in most other specimens except some from the Meseta Central, in which the throats are heavily flecked with black. This variation occurs in males and females.

**TADPOLES:** Eight tadpoles in developmental stage 36 have body lengths of 10.2 to 11.7 (mean, 10.8) mm. and total lengths of 29.5 to 34.5 (mean, 32.3) mm. A typical tadpole in this stage has a body length of 11.7 mm. and a total length of 34.5 mm. The body is about three-fourths as deep as wide; the snout is broadly rounded in dorsal view, sloping and rounded in lateral view. The nostrils are slightly closer to the eyes than to the tip of the snout. The eyes are widely separated and directed dorsolaterally. The spiracle is sinistral and ventral to the midline; the spiracular opening is directed dorsolaterally at a point about two-thirds the length of the body. The mouth is ventral; the cloacal tube is short and dextral. The caudal musculature is heavy and straight. The dorsal fin does not extend onto the body and is deepest at about the midlength of the tail. At that point the depth of the dorsal and ventral fin is about equal (fig. 284F).

The mouth is large and has well-developed lateral folds. The entire upper and lower lips are bordered by two rows of small papillae; additional papillae are present in the lateral fold. The upper beak is robust; the inner surface is curved so as not to form a continuous arch with the slender lateral processes. The lower beak is robust; both beaks bear blunt serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length, and the second row is narrowly interrupted medially. The three lower rows are complete and nearly as long as the upper rows. Usually the lower rows are deeply indented medially (fig. 285F).

The body is tan; in some individuals there is an olive-tan tinge. The caudal musculature is tan with dull red or reddish brown flecks and dashes, which tend to form a crossbar pattern on the dorsal surface of the caudal musculature. Bluish green flecks are present on the sides of the body in some individuals. Usually the belly is pale tan with a silvery

white tint, but in some specimens the belly is silvery golden. The iris is bronze.

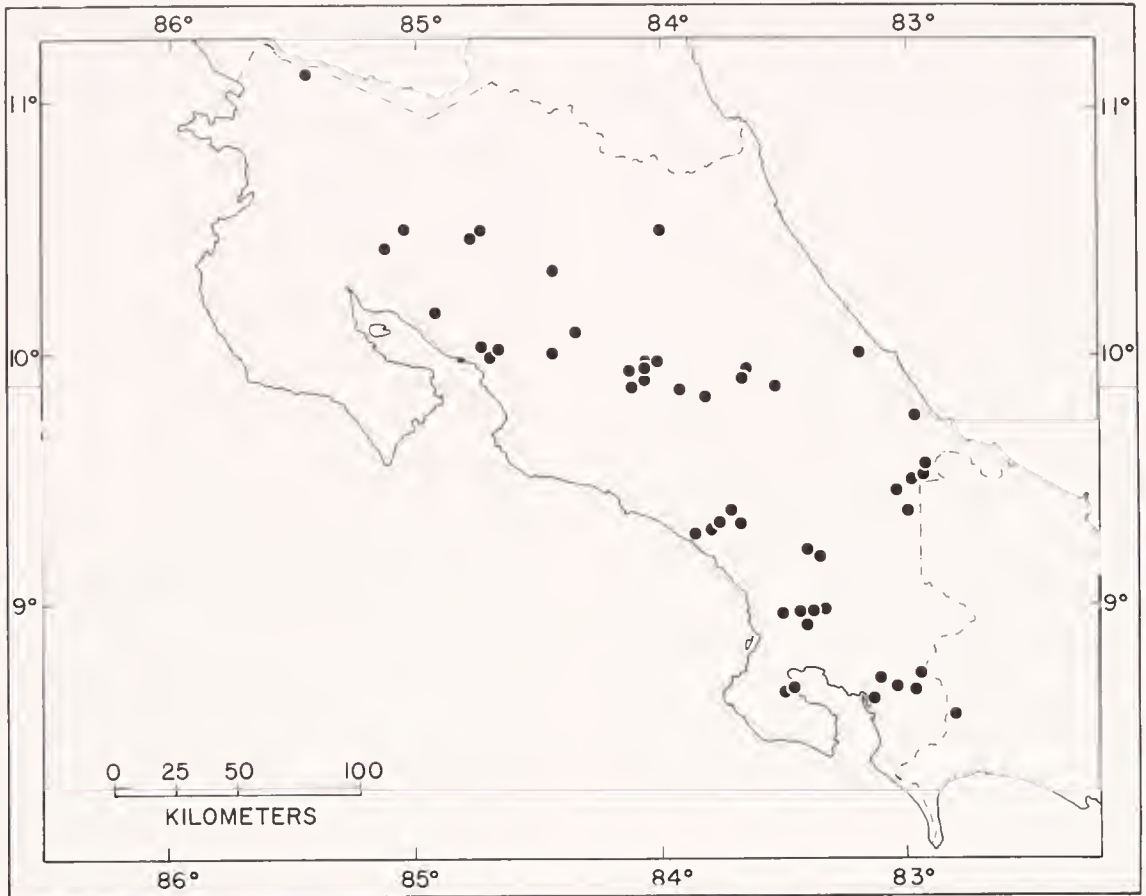
**MATING CALL:** The call of *Smilisca sordida* consists of one to six moderately short, rather high-pitched notes repeated at intervals of 12 seconds to several minutes. The duration of each note is 0.18 to 0.45 (mean, 0.29) seconds. Each note is a vibrant rattle having 78 to 135 (mean, 105) pulses per second. The fundamental frequency is 90 to 140 (mean, 123) cycles per second. Two frequency bands are emphasized; these major frequencies are at about 1215 and 2695 cycles per second (pl. 33, fig. 3).

**NATURAL HISTORY:** *Smilisca sordida* lives in the vicinity of rocky streams having low gradients. Breeding takes place primarily in the dry season, when the water in the streams is clear and at a low level. Throughout most of the range of *S. sordida*, showers or even short heavy rains, occur in the dry season. After such rains the breeding activity is maximum. Breeding congregations have been found from December to April. Males usually call from rocks or gravel bars in, or at the edge of, streams. Some individuals perch in low bushes overhanging the streams, and some sit in shallow pools in the streams. Claspings pairs have been found on the banks of streams and shallow water in streams. The tadpoles live in shallow parts of the stream, where they cling to the surfaces of small rocks and hide beneath leaves and rocks. Nine recently metamorphosed young have snout-vent lengths of 13.1 and 15.7 (mean, 14.9) mm.

**REMARKS:** Duellman and Trueb (1966, p. 328) discussed the systematic status of the various names that have been applied to the frogs here called *Smilisca sordida*. Most references to this Costa Rican species are found under the name of *Hyla gabbii*.

**ETYMOLOGY:** The specific name *sordida* is derived from the Latin *sordidus* meaning "dirty" and apparently refers to the dull, grayish brown dorsal color of many preserved specimens of this species.

**DISTRIBUTION:** *Smilisca sordida* occurs along the Pacific slopes and lowlands from Guanacaste, Costa Rica, southeastward to extreme western Panamá. It occurs to elevations of about 1200 meters on the Meseta Cen-

FIG. 291. Distribution of *Smilisca sordida*.

tral in Costa Rica and on the Caribbean slopes and lowlands of Costa Rica and probably adjacent Panamá (fig. 291). One specimen reportedly comes from "Río Grande, Nicaragua."

See Appendix 1 for the locality records of the 465 examined.

#### Genus *Pternohyla* Boulenger

*Pternohyla* Boulenger, 1882b, p. 326 [type species, *Pternohyla fodiens* Boulenger, 1882a, by monotypy].

GENEROTYPE: *Pternohyla fodiens* Boulenger, 1882b.

ETYMOLOGY: The generic name is derived from the Greek *pterna*, meaning heel, and *Hylas*, a character in Greek mythology. The generic name is in reference to the spade-like inner metatarsal tubercle.

DEFINITION: Frogs of the genus *Pterno-*

*hyla* are medium in size and have a pale brown dorsum with dark brown dorsal markings. The pupil is horizontal, and the palpebral membrane is not reticulated. The limbs are short; the fingers lack webbing, and the toes are less than half webbed. The terminal discs are small, and the inner metatarsal tubercle is large. The vocal sac is subgular and paired. Breeding males have horny nuptial excrescences on the thumbs. The skin of the head is partly co-ossified with the underlying cranial elements. The canthal ridges are pronounced, and the maxillaries are expanded laterally to form a labial shelf. The skull is as wide as, or slightly wider than, long. A prenasal bone is absent, but an internasal is present in one species. The squamosal-maxillary arch is complete, and quadratojugals are present. The palatines are robust and articu-

late with the sphenethmoid. The medial ramus of the pterygoid is reduced and does not articulate with the prootic. Bifid, spatulate teeth are present on the premaxillaries, maxillaries, and prevomers; the palatines and parasphenoid are edentate. The tadpoles are short-tailed pelagic types with an anteroventral mouth having robust beaks and large papillae laterally and ventrally. The long, pointed teeth are arranged in two upper and three lower rows. The mating call consists of a series of short notes resembling the quacking of a duck. The haploid number of chromosomes is 12 (known only in *fodiens*).

COMPOSITION OF GENUS: Two monotypic species are recognized; both occur in western México. I have examined 630 preserved frogs, 13 skeletons, and three lots of tadpoles of *Pternohylla* from México and one frog from Arizona.

ANALYSIS OF CHARACTERS: The two species differ from one another in several external characters. *Pternohylla fodiens* has proportionately longer legs and feet and a proportionately large head (see ratios given in the accounts of the species). The head is about as wide as long in *dentata* and wider than long in *fodiens*. The latter has a proportionately smaller tympanum than *dentata*. The fingers and toes of *dentata* are robust and lack expanded discs. The inner metatarsal tubercle is large, elliptical, and rounded in section in *dentata*, whereas the tubercle is larger, ovoid, flattened in section, and has an elevated outer edge in *fodiens* (fig. 292).

Both species have dark vocal sacs. Those of *fodiens* are dark gray or black with the tips of granules white, thereby giving a white-speckled appearance. The sacs of *dentata* are grayish brown. In breeding males the two halves of the vocal sac are closely approximated in *fodiens* and broadly separated by granular skin in *dentata* (fig. 293).

Integumentary-cranial co-ossification is incomplete. The nasal at the anterior edge of the orbit, the sphenethmoid, and the dorsal part of the prootic are not co-ossified in either species. The dermal roofing bones are more extensively ossified in *fodiens* than in *dentata*. In the former the more greatly expanded labial flanges result in a proportionately broader skull, and the larger nasals and fronto-

parietals result in less of the sphenethmoid being exposed dorsally than in *dentata*. The premaxillaries are more robust and are involved in co-ossification in *fodiens*, and the snout region is further modified by the presence of an internasal (Trueb, 1970a), a dermal bone medial to the external nares and the anterior tips of the nasals. The dorsal surface of the internasal is involved in integumentary-cranial co-ossification (fig. 294).

DISTRIBUTION: Frogs of the genus *Pternohylla* occur in xeric environments from south-central Arizona in the United States southward through western México to the Tepalcatepec Valley in Michoacán.

DISCUSSION: The adaptive trends in *Pternohylla* have been towards a fossorial existence, as illustrated by the modifications in the limbs and head and by the squat, toad-like form of the body. Although both species have these modifications, certain specializations have been carried farther in one species than in the other. For example, the limbs are proportionately shorter and the terminal discs on the digits are further reduced in *dentata* than in *fodiens*. In the latter the integumentary-cranial co-ossification of the skull is more nearly complete, and the inner metatarsal tubercle is more specialized than in *dentata*. The bony internasal ridge in *fodiens* seems to be analogous to the boss on the snout in some species of *Bufo* and *Scaphiopus*. Likewise, the inner metatarsal tubercle in *fodiens* is spatulate like that in *Scaphiopus* and some *Bufo*, although in *fodiens* the tubercle is not horny.

Trueb (1970a) showed the cranial characters of *Pternohylla* could be derived from those of *Smilisca baudinii* and that osteologically *P. dentata* is somewhat intermediate between *S. baudinii* and *P. fodiens*. *Smilisca baudinii* has paired, subgular vocal sacs and an enlarged inner metatarsal tubercle. The tadpoles and mating call of *Pternohylla* are not greatly different from those of *Smilisca baudinii*. Furthermore, Starrett (1960b) suggested a close relationship of the two genera on the basis of the identical jaw musculature. Thus, it seems likely that *Pternohylla* evolved from a *Smilisca baudinii* stock and that the evolutionary trends were towards adaptation for a fossorial existence in xeric environments.





FIG. 292. Hands and feet of *Pternohyla*. A and C. *P. dentata*, K.U. No. 60081. B and D. *P. fodiens*, K.U. No. 78463.  $\times 6$ .

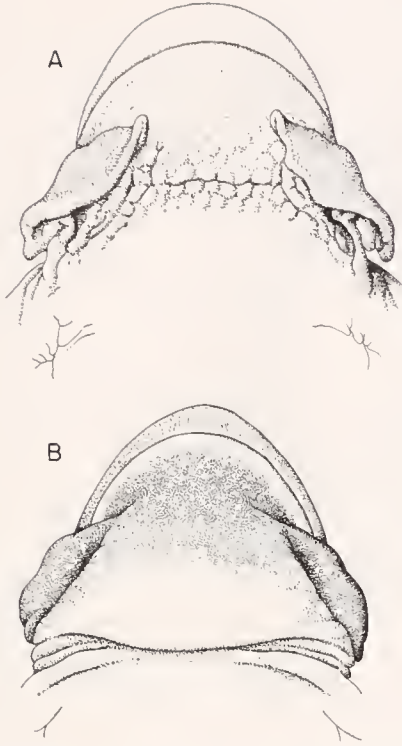


FIG. 293. Ventral views of throats of breeding males of *Pternohyla*. A. *P. dentata*, K.U. No. 60083. B. *P. fodiens*, K.U. No. 78463.  $\times 2$ .

Duellman and Trueb (1966) hypothesized that the species of *Smilisca* probably had differentiated from one another by the end of the Pliocene, at which time *S. baudinii* inhabited the Pacific lowlands of México. Increasing aridity throughout the Pleistocene probably was the environmental impetus that resulted in the differentiation of a fossorial stock which gave rise to *Pternohyla*. Apparently *P. dentata* represents a population of the *Pternohyla* stock that was formerly isolated in the upper Río Santiago Basin on the Mexican Plateau.

#### *Pternohyla dentata* Smith

*Pternohyla dentata* Smith, 1957, p. 1 [holotype, U.I.M.N.H. No. 40551 from 8 miles northeast of Lagos de Moreno, Jalisco, México; W. H. Davis, W. Z. Lidicker, and John R. Winkelmann collectors].

**DIAGNOSIS:** This moderate-sized, casque-headed frog is characterized by incomplete integumentary-cranial co-ossification and the absence of an internasals. It is readily distin-

guished from *Pternohyla fodiens* by having a rounded inner metatarsal tubercle and narrow tips of the digits, whereas *fodiens* has a spade-like inner metatarsal tubercle and distinct terminal discs on the digits. Furthermore, *fodiens* has the two halves of the vocal sac connected medially and an internasals ridge resulting in an acutely rounded snout; *dentata* has the two halves of the vocal sac broadly separated medially and lacks an internasals ridge, thereby having a bluntly rounded snout. Of the other Middle American casque-headed hylids, *Anotheca* lacks labial flanges and has long cranial spines, and *Triprion* has a broad labial flange, a large prenasal bone, and large terminal discs on the digits.

**DESCRIPTION:** In a series of 25 males from Aguascalientes, México, the snout-vent length is 47.6 to 62.1 (mean, 52.4) mm.; the ratio of tibia length to snout-vent length is 0.311 to 0.360 (mean, 0.344); the ratio of foot length to snout-vent length is 0.320 to 0.370 (mean, 0.351); the ratio of head length to snout-vent length is 0.275 to 0.313 (mean, 0.294); the ratio of head width to snout-vent length is 0.268 to 0.310 (mean, 0.291), and the ratio of the diameter of the tympanum to that of the eye is 0.604 to 0.767 (mean, 0.660). Three females from the same locality have snout-vent lengths of 52.7 to 54.0 (mean, 53.4) mm. They do not differ significantly from the males in any proportions.

The head is about as wide as long and noticeably narrower than the body. In dorsal profile the snout is bluntly rounded; in lateral profile it is acutely rounded and protruding beyond the leading edge of the lower jaw. The snout is moderately long and somewhat spatulate. The nostrils are protuberant, directed dorsally, and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthal ridge is elevated and terminates just posterior to the nostrils. The loreal region is deeply concave, and the lips are broad and flared. The entire labial region is moderately expanded; the expanded lips extend posteriorly to the tympanum. A bony ridge extends posteriorly from the orbit, above the tympanum, and continues as a dermal fold to a point above the insertion of the arm. The skin on the skull is co-ossified with the underlying dermal bones,

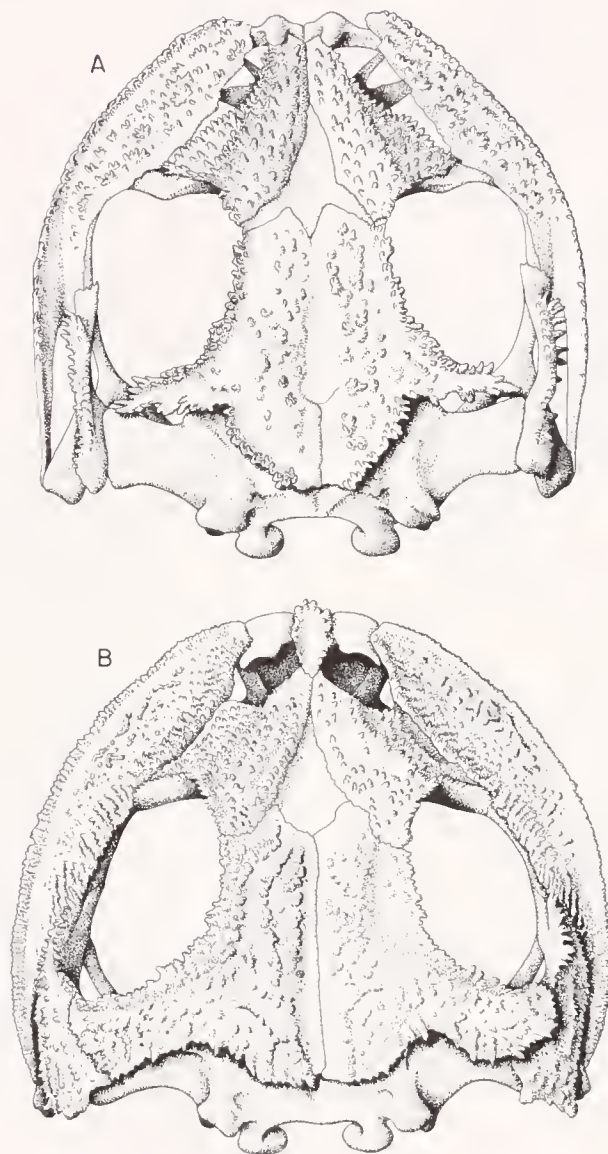


FIG. 294. Dorsal views of the skulls of *Pteronohyla*.  
A. *P. dentata*, K.U. No. 106291. B. *P. fodiens*, K.U. No. 86615.  $\times 5$ .



except in the region of the frontoparietal fontanelle, the sphenethmoid, the nasals immediately anterior to the orbit, and the outer edges of the maxillaries. There is no distinct internasal ridge extending to the tip of the snout. The upper edge of the tympanum is concealed by the bony supratympanic ridge, and the posterior edge is concealed by granular skin in some specimens; otherwise the tympanum is distinct and separated from the eye by a distance equal to about one-half of the diameter of the tympanum.

The arms are short and robust. There are no tubercles along the ventrolateral edge of the forearm, but a thin transverse dermal fold is present on the wrist. The fingers are short, robust, and lack terminal discs. The tips of the fingers are bluntly rounded. The subarticular tubercles are large and round; none is bifid. Faint supernumerary tubercles are present on the proximal segments of the third and fourth fingers in some specimens. A broad, diffuse palmar tubercle is present; the prepollex is moderately enlarged and, in males, bears a thin nuptial excrecence. The thumb is nearly as long as the second finger, and webbing between the fingers is absent (fig. 292A). The legs are short. The heels of the adpressed limbs overlap by about one-fourth of the length of the shank; the tibiotarsal articulation extends to the axilla. A distinct transverse dermal fold is present on the heel, and a distinct, elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is elongate, elliptical, and round in section. The outer metatarsal tubercle is small and subconical. The toes are moderately short, slender, and lack terminal discs. The subarticular tubercles are moderately large and round; small, usually indistinct supernumerary tubercles are present on the proximal segment of each digit. The toes are webbed only basally (fig. 292C).

The anal opening is directed posteriorly at the level of the upper edge of the thighs; no anal flap is present. The skin on the dorsal surfaces of the body is weakly granular, and that on the dorsal surfaces of the limbs and the ventral surfaces of the forelimbs, shanks, and feet is smooth. The skin on the belly and ventral surfaces of the thighs is heavily granular. The tongue is broadly cordiform,

shallowly notched behind, and free posteriorly for about one-third of its length. The denticulate processes of the prevomers are small transverse elevations between the small round choanae. There are four to six teeth on each process, and the total number of prevomerine teeth is eight to 12 (mean, 10.3). The vocal slits extend from the posterolateral base of the tongue nearly to the angles of the jaws. The vocal sac is paired and subgular; the halves of the sac are connected by a narrow tube, but there is a broad separation of granular skin between the two halves of the sac.

The color in life is unknown. In preservative the dorsal surfaces of the body and limbs are grayish brown to pale reddish brown with dark brown to reddish brown spots and longitudinal markings (pl. 2, fig. 1). In those individuals having reddish brown blotches, the blotches are narrowly outlined by dark brown or black. Most individuals have dark spots on the upper eyelids and a dark dash on the head anterior to the eyes. Dark bars are present on the upper lips. The dorsal markings are either discrete spots irregularly arranged in about four longitudinal rows or consist of fused spots which form broad longitudinal stripes. The most common pattern of fused spots consists of a pair of paravertebral stripes and a row of dorsolateral spots. The flanks are creamy tan with dark brown spots. Brown blotches or transverse bars are present on the limbs. There are two or three such bars on each shank and thigh, and usually two on the foot and forearm. The posterior surfaces of the thighs are creamy white with brown flecks and dashes. The venter is creamy yellow, and the vocal sacs are brownish gray.

**TADPOLES:** The tadpoles of *Pterohyla dentata* are unknown.

**MATING CALL:** Recordings of the call of this species are not available; consequently it can not be described and compared with that of *P. fodiens*.

**NATURAL HISTORY:** Little is known about the natural history of this species. According to Smith (1957, p. 4) the holotype was found in a temporary road-side pond in high plateau country characterized by short-grass plain with scattered xeric shrubs. Chrapliwy, Wil-

liams, and Smith (1961, p. 87) reported on the large series from Aguascalientes and stated: "All were taken on the night of July 21 from a flooded field with rain water level varying from one to four inches in depth. Rain had fallen intermittently in the day and evening. The frogs, in chorus, were not wary and often continued to call after being picked up. Several pairs were observed in amplexus."

REMARKS: Smith (1957) in his description of *Pternohyla dentata* diagnosed this species as having no bony labial fringe and by possessing parasphenoid teeth. Smith apparently referred to the outer edge of the lips as the "labial fringe"; the outer edge of the lips are not involved in integumentary-cranial co-ossification, but the dorsal surfaces of the expanded maxillaries are involved in co-ossification. Despite the statement of Smith, parasphenoid "teeth" are absent in this species. Furthermore, Smith (1957, p. 3) stated: "The species *P. dentata* possesses both parasphenoid and palatal 'teeth,' like *Diaglena* and *Triprrion* whereas *P. fodiens* lacks them." Odontoids are present on the palatines in *Triprrion spatulatus* and on the parasphenoid in both species of *Triprrion*. The palatines and parasphenoid are edentate in both species of *Pternohyla*.

ETYMOLOGY: The specific name is Latin meaning tooth and refers to the supposed presence of parasphenoid teeth in this species.

DISTRIBUTION: *Pternohyla dentata* is known from the upper Río Santiago Basin in southern Aguascalientes and northern Jalisco, México, at elevations of 1800 to 1900 meters (fig. 295).

See Appendix 1 for the locality records of the 148 specimens examined.

### *Pternohyla fodiens* Boulenger

*Pternohyla fodiens* Boulenger, 1882b, p. 326 [holotype, B.M.N.H. No. 1947.2.24.26 from Presidio, Sinaloa, México; Alphonso Forrer collector]. Günther, 1901 (1885-1902), p. 292. Kellogg, 1932, p. 135 [synonymized *Hyla rudis* Mocquard, 1899a, with *Pternohyla fodiens* Boulenger, 1882b]. Smith and Taylor, 1948, p. 71.

*Hyla rudis* Mocquard, 1899a, p. 163 [holotype, M.N.H.N. No. 373a from Guadalajara, Jalisco, México; Léon Diguët collector].

DIAGNOSIS: This moderate-sized, casque-headed frog is characterized by incomplete

integumentary-cranial co-ossification and the presence of an internasal. The species is readily distinguishable from *Pternohyla dentata* by having a spade-like inner metatarsal tubercle, terminal discs on the digits, a median connection between the two halves of the vocal sac, and an internasal ridge resulting in an acutely rounded snout. *Pternohyla dentata* has a rounded inner metatarsal tubercle and a broad separation between the vocal sacs, and lacks terminal discs on the digits and an internasal ridge. Of the other Middle American casque-headed hylids, *Anotheca* lacks labial flanges and has long cranial spines, and *Triprrion* has a broad labial flange, a large prenasal bone, and large terminal discs on the digits.

DESCRIPTION: Males of this moderate-sized species attain a maximum snout-vent length of 62.6 mm., and females reach 63.7 mm. In a series of 20 males from southern Sinaloa, México, the snout-vent length is 40.7 to 62.6 (mean, 49.4) mm.; the ratio of tibia length to snout-vent length is 0.355 to 0.409 (mean, 0.388); the ratio of foot length to snout-vent length is 0.374 to 0.507 (mean, 0.417); the ratio of head length to snout-vent length is 0.289 to 0.344 (mean, 0.326); the ratio of head width to snout-vent length is 0.324 to 0.361 (mean, 0.341), and the ratio of the diameter of tympanum to that of the eye is 0.582 to 0.659 (mean, 0.621). Four females from the same locality have snout-vent lengths of 60.0 to 62.3 (mean, 61.1) mm. They do not differ significantly from the males in proportions.

The head is relatively small and slightly wider than long, but narrower than the body. In dorsal profile the snout is acutely rounded; in lateral profile it is bluntly rounded. The snout is moderately long, and the nostrils are protuberant and situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthal ridges are elevated and meet just posterior to the level of the nostrils, from which point an elevated, bony internasal ridge extends anteriorly to the tip of the snout. The loreal region is slightly concave, and the lips are broad and flared; the flared lips extend posteriorly to the tympanum. Bony pretympanic and supratympanic ridges are present; a thin dermal



FIG. 295. Distribution of *Pternohyla dentata* and *Pternohyla fodiens*.



fold extends posteroventrally from the terminus of the supratympanic ridge. The upper edge is concealed beneath the supratympanic ridge, and the tympanum is separated from the eye by a distance nearly equal to the diameter of the tympanum. The skin is co-ossified with most of the underlying cranial elements, except in the region of the frontoparietal fontanelle, sphenethmoid, and nasals immediately anterior to the orbits; also the edge of the upper lip is not co-ossified.

The arms are moderately short and robust; no tubercles are present on the ventrolateral edge of the forearm, but a thin, indistinct in some specimens, transverse fold is present on the wrist. The fingers are moderately long and slender and have small discs; the diameter of the disc on the third finger is equal to about one-half of the diameter of the eye. The subarticular tubercles are large and round; none is bifid. Indistinct supernumerary tubercles are present on the proximal segments of the digits in most specimens. A flat, partially bifid, diffuse palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a thin horny nuptial excrescence. Webbing is absent between the fingers (fig. 292B). The hind limbs are short and robust; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the point of the insertion of the arm. A thin transverse dermal fold is present on the heels, and a narrow tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, elliptical, and spade-like with an elevated outer edge. The outer metatarsal tubercle is moderately small and subconical. The toes are relatively long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately large and round; small, indistinct, supernumerary tubercles are present on the proximal segments of each digit. The toes are webbed basally (fig. 292D).

The anal opening is directed posteriorly at the level of the upper level of the thighs. A short anal flap is present. The skin on the dorsum is minutely corrugated or weakly granular; that on the belly and proximal segments of the thighs is granular and the skin on the other ventral surfaces and the dorsal

surfaces of the limbs is smooth. The tongue is broadly cordiform, shallowly notched behind, and free posteriorly for about one-fourth of its length. The denticerous processes of the prevomers are small, elliptical, transverse ridges between the posterior margins of the small round choanae. Males have four to six teeth on each process and a total of eight to 12 (mean, 10.3) prevomerine teeth. Females have five to seven teeth on each process and a total of 11 to 13 (mean, 12.1) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue nearly to the angles of the jaws. The vocal sac is subgular and paired; the two halves are narrowly separated medially.

The general coloration of adults of *Pternohyla fodiens* is tan or pale brown with dark brown markings (pl. 72, fig. 4). The dorsum varies from tan to pale olive-brown, grayish brown, or pinkish brown. The dorsal markings are dark brown or reddish brown outlined with dark brown or black. Most individuals have a dark spot on the head anterior to the eyes, a dark stripe along the canthal ridge, and dark vertical bars on the lips. A dark mark usually extends posteriorly from the tympanum to a point above the insertion of the arm. The markings on the back vary from longitudinal dark stripes to many small dark spots. The flanks are creamy tan with dark brown reticulations. The dorsal surfaces of the limbs are tan with dark brown or reddish brown transverse bars. The posterior surfaces of the thighs are brown with creamy yellow flecks, spots, or dashes. The venter is white, except for the vocal sac in breeding males, which is grayish brown. The iris is dull bronze with fine black reticulations.

Juveniles are pale green above with scattered brown flecks or spots (pl. 72, fig. 5). The flanks and posterior surfaces of the thighs are dark brown. These small specimens are colored very much like the adults of *Hyla eximia*.

In preservative, the dorsal ground color is pale grayish brown, creamy tan, or pinkish tan. The dorsal markings are dark brown. The venter is creamy white, except for the vocal sac which is dark gray with white flecks. The flecks are on the tips of the small granules in the vocal sac.



FIG. 296. Tadpole of *Pternohyla fodiens*, K.U. No. 104193.  $\times 4$ .

**TADPOLES:** A typical tadpole in developmental stage 26 has a total length of 29.2 mm. and a body length of 12.3 mm. The body is as wide as deep. In dorsal profile the snout is bluntly rounded, and in lateral profile, more acutely rounded. The nostrils are directed anterolaterally and situated about midway between the eyes and the tip of the snout. The eyes are moderately small, situated dorsolaterally and directed laterally. The spiracular opening is on the level of the midline about two-thirds of the distance from the snout to the posterior end of the body. The anal tube is dextral and moderately long. The caudal musculature is slender and terminates just short of the tip of the caudal fins. The dorsal fin does not extend onto the body; at mid-length of the tail the depth of the caudal musculature is slightly less than the depth of either the dorsal or ventral fin (fig. 296).

In life both the body and tail are dull tan with olive-brown mottling. The belly is dusty white. In preservative the body is dark brown and the caudal musculature is creamy tan with dark brown flecks, which are also present on the caudal fin.

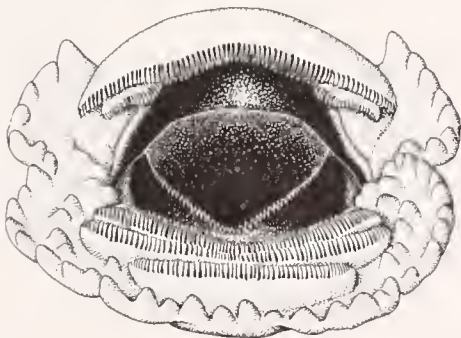


FIG. 297. Mouth of tadpole of *Pternohyla fodiens*, K.U. No. 104196.  $\times 25$ .

The mouth is small, anteroventral in position and direction. The median part of the upper lip is bare; large, partially fused labial papillae are present in a single row midventrally and anterolaterally, and in two rows laterally. The lips are folded laterally. The beaks are robust and bear small, pointed serrations. There are two upper and three lower rows of teeth. All of the teeth are moderately long and pointed. The second upper row is broadly interrupted medially. The lower rows are complete; the first and second lower rows are nearly as long as the first upper row, whereas the third lower row is noticeably shorter (fig. 297).

Webb (1963) described small tadpoles and later developmental stages from Sinaloa; he mentioned metamorphosing individuals having lengths of 18 to 24 mm. (including tail stubs).

**MATING CALL:** The call of *Pternohyla fodiens* consists of a series of low-pitched notes, resembling the quacking of a duck. The notes are quickly repeated; the note repetition rate is 81 to 115 (mean, 95) notes per minute. The notes have a duration of 0.21 to 0.28 (mean, 0.25) of a second and a pulse rate of 118 to 125 (mean, 122) pulses per second. The fundamental frequency is 122 to 134 (mean, 126) cycles per second and the dominant frequency is 2200 to 2278 (mean, 2230) cycles per second (pl. 34, fig. 1).

**NATURAL HISTORY:** *Pternohyla fodiens* inhabits arid tropical scrub forests where it breeds in temporary pools formed by rains which fall in the months of June through September. Males usually call near temporary ponds, but not at the edge of the water. The frogs call from secluded places such as under the edge of a rock, at the bases of bushes, or in clumps of grass.

Hardy and McDiarmid (1969) reported on the tadpoles of this species from La Cruz, Sinaloa. They stated: "Thousands of tadpoles, all of which appeared to be newly hatched and about 10 mm. in length, were all that remained from the previous night's breeding activity. Most of the larvae were floating in clusters with their tail pointing downward from the surface of the pond. When a cluster was disturbed, the larvae would disperse, some swimming away and others sinking to the bottom. Jelly envelopes, some containing undeveloped eggs were scattered over the bottom of the pond. The tadpoles clustered at the surface may have been feeding on surface scum. Three large series were collected and allowed to develop. Three days later the larvae lost their external gills."

I obtained larvae of the species in a shallow, grassy pond, 34 kilometers north-northwest of Tepic, Nayarit.

REMARKS: Firschein (1951) noted the phragmotic behavior and "Unken reflex" in this species. I have observed the same behavior in this frog. Individuals when disturbed, flex the head downward and elevate the limbs so as to rest on the belly. The fossorial habits of *Pternohyla* indicate that the phragmotic behavior is not for the purpose of closing holes in trees as it is for *Triprrion*, but more likely the head is used for closing burrows in the ground.

*Pternohyla fodiens* was only recently discovered in the United States (Chrapliwy and Williams, 1957).

Kellogg (1932) showed that the type of *Hyla rudis* Moequard (1899a) is a young individual of *Pternohyla fodiens*. As noted previously, the coloration of the juveniles is noticeably different from that of the adults. Furthermore, juveniles lack integumentary-cranial co-ossification.

ETYMOLOGY: The specific name *fodiens* is the genitive of the Latin *fodio*, meaning to dig or to dig up and apparently refers to the supposed digging adaptations of the spadec-like inner metatarsal tubercles.

DISTRIBUTION: *Pternohyla fodiens* inhabits xeric regions from south-central Arizona in the United States southward through western Sonora and the coastal regions of Sinaloa, and thence into the foothills of the Pacific

slopes of the Sierra Madre Occidental in Nayarit and southward onto the Mexican Plateau in Jalisco. This species also occurs on the Colima Plateau and in the Tepalcatepec Valley in Michoacán, México (fig. 295). This species occurs at elevations from sea level to about 1500 meters.

See Appendix 1 for the locality records of the 498 specimens examined.

### Genus *Triprrion* Cope

*Pharyngodon* Cope, 1865b, p. 193 [type species *Pharyngodon petasatus* Cope, 1865b, by monotypy; preoccupied by *Pharyngodon* Diesing, 1861 (Nemathelminthes)].

*Triprrion* Cope, 1866a, p. 127 [replacement name for *Pharyngodon* Cope, 1865b, preoccupied].

*Diaglena* Cope, 1887, p. 12 [type species, *Triprrion spatulatus* Günther, 1882, by monotypy].

GENEROTYPE: *Pharyngodon* (= *Triprrion*) *petasatus* Cope, 1865b.

ETYMOLOGY: The generic name is derived from the Greek *trion*, meaning three and the Greek *prion*, meaning saw, and is in reference to the serrate labial fringes anteriorly and laterally.

DEFINITION: The frogs in this genus are moderately large to large and are characterized by integumentary-cranial co-ossification and a casqued head that is longer than broad (fig. 298). The dorsum is olive-green to yellowish tan and uniformly colored or marked with blotches or reticulations. The pupil is horizontally elliptical, and the palpebral membrane is clear. The fingers are webbed basally, and the toes are about two-thirds webbed. Moderately large terminal discs are present on the digits, and a large,



FIG. 298. Lateral view of the head of *Triprrion petasatus*, K.U. No. 71503, showing casqued head.  $\times 3$ .



elliptical inner metatarsal tubercle is present. The vocal sac is single, median or paired, and subgular or bilobate and situated posteriorly on the throat. The tongue is round. Breeding males have horny nuptial excrescences on the thumbs. The skin is completely co-ossified with the underlying cranial elements. A large prenasal and the laterally expanded maxillaries form a broad, serrate, labial shelf (fig. 299). The premaxillaries are partly hidden by the prenasal, and the alary processes of the premaxillaries are rotated anteriorly. The skull is completely roofed; a dermal sphenethmoid is present or absent. The squamosals are in bony contact with the maxillaries, and the quadratojugals are well developed. The palatine is slender, and the medial ramus of the pterygoid is reduced and attached to the prootic only by connective tissue. Teeth are present on the premaxillaries, maxillaries, and prevomers, and odontoids are present on the parasphenoid and present or absent on the palatines. The teeth are spatulate and bifid. The tadpoles are pelagic types with anteroventral mouths and deep caudal fins. The mating call consists of a single, low-pitched note. The chromosome number is  $n = 12$ ,  $2n = 24$  (known only in *petasatus*).

COMPOSITION OF THE GENUS: Two species (*petasatus* and *spatulatus*), the latter with two subspecies, comprise the genus; both are Middle American endemics. Of the two species, 791 preserved frogs, 28 skeletons, nine lots of tadpoles, and four preserved clutches of eggs have been examined.

ANALYSIS OF CHARACTERS: The principal specific characters of the frogs in the genus *Triprion* are those of the casque head. A dermal sphenethmoid is present in *petasatus* and absent in *spatulatus*; in the former the canthal ridges are nearly perpendicular to the body axis, whereas in *spatulatus* the ridges are inclined anteromedially. The snout is upturned in *petasatus* and nearly straight in *spatulatus*, and the latter has slender palatines that bear odontoids, whereas in *petasatus* the palatines are greatly reduced. The vocal sac is single and median in *spatulatus* and paired in *petasatus*. In both species the vocal sac is situated on the posterior part of the throat. The structure of the hands and feet in the two species is nearly identical (fig. 300).

DISTRIBUTION: The species of *Triprion* inhabit xeric areas on the Pacific lowlands of México from central Sinaloa to the Isthmus of Tehuantepec and in the Yucatan Peninsula southward to central El Petén, Guatemala.

DISCUSSION: The phylogenetic relationships of the casque-headed hylids were discussed by Trueb (1970a), who provided evidence that *Diaglena* and *Triprion* were congeneric. Furthermore, she showed that the South American casque-headed hylid genera, *Aparasphenodon*, *Corythomantis*, *Osteocephalus*, *Trachycephalus*, and *Tetraprion* were not related to *Triprion*. Likewise, the Mexican genus *Pternohyla*, although probably phylogenetically closer to *Triprion* than are the South American genera, represents a phyletic line that is less advanced in adaptive cranial modifications.

*Triprion* evidently was more widespread in México and northern Central America prior to the Pleistocene. The present distribution of the species is a relictual pattern that is common among xeric restricted species and is the result of isolation due to changing environmental conditions in the Pleistocene (Duellman, 1960b and 1966c). *Triprion petasatus* is more highly specialized than *spatulatus*; this specialization is evident in the more highly modified skull—presence of a dermal sphenethmoid, reduction of palatines, and higher canthal ridges.

### *Triprion spatulatus* Günther

*Triprion spatulatus* Günther, 1882, p. 279 [syntypes B.M.N.H. Nos. 1947.2.25.79-1947.2.25.81 from Presidio de Mazatlán, Sinaloa, México; Alphonso Forrer collector].

DIAGNOSIS: This is a large species (males to 87 mm.; females to 101 mm.) that is readily distinguished from other Middle American casque-headed hylids by having a large prenasal, greatly expanded maxillaries, odontoids on the palatines, no spines on top of the head and no dermal sphenethmoid. *Triprion petasatus* differs by having a dermal sphenethmoid, the tip of the snout upturned and by lacking odontoids on the palatines. *Pternohyla* has only moderate labial flanges, and lacks a dermal sphenethmoid and prenasal. Furthermore, *Pternohyla* is squat and toad-like in appearance and has a spade-like inner

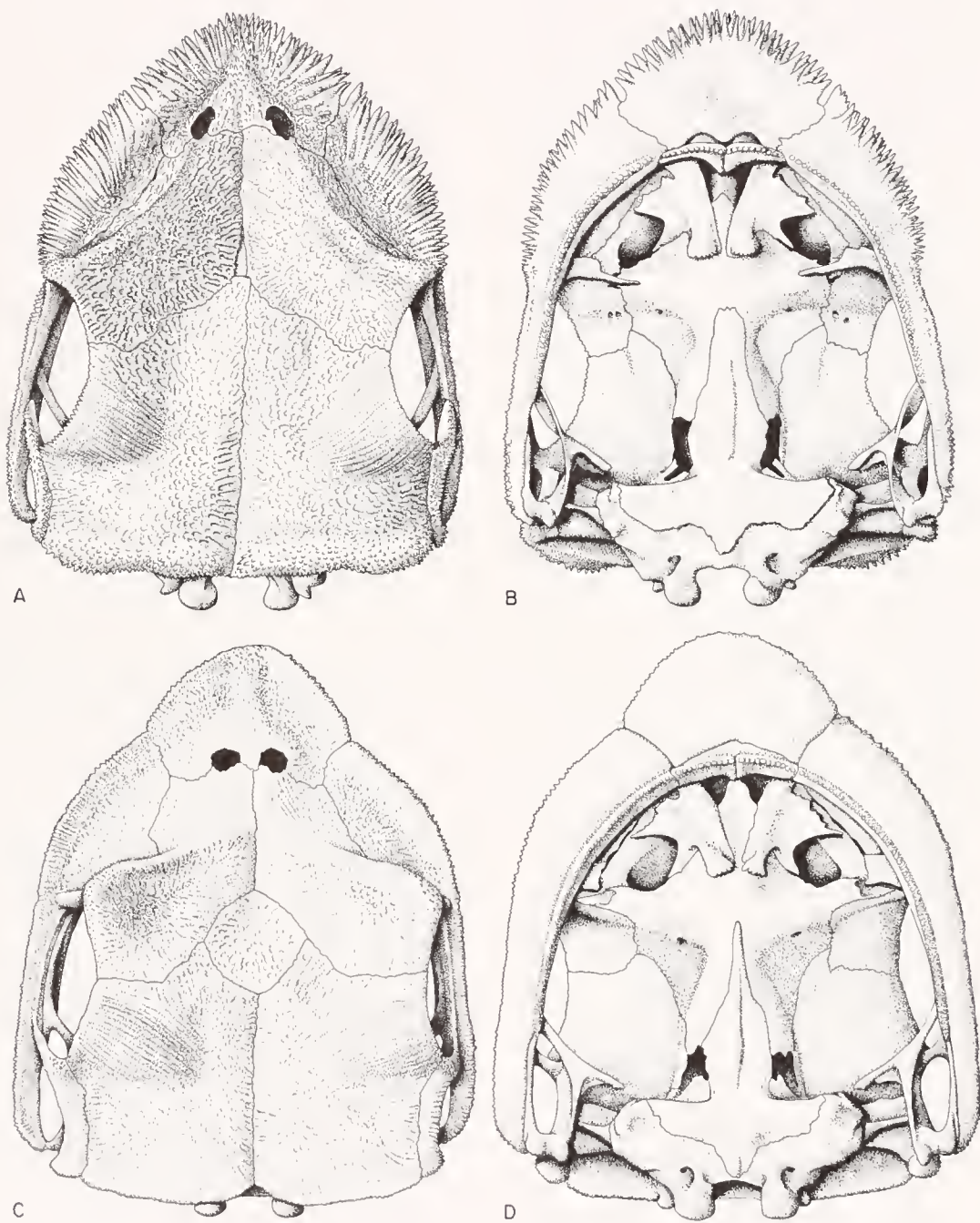


FIG. 299. Skulls of *Triprion*. A, Dorsal and B, Ventral of *T. spatulatus*, K.U. No. 84904; C, Dorsal and D, Ventral of *T. petasatus*, K.U. No. 71780.  $\times 3$ .



FIG. 300. Hands and feet of *Tripurion*. A and B. *T. spatulatus*, U.M.M.Z. No. 115322. C and D. *T. petasatus*, K.U. No. 71503.  $\times 3.5$ .



metatarsal tubercle. *Anothea* lacks labial flanges and has spines on the supratympanic and occipital ridges.

CONTENT: Two subspecies are recognized: *T. spatulatus spatulatus* Günther and *T. spatulatus reticulatus* Taylor.

REMARKS: Although minor differences in proportions exist, the subspecies are most readily distinguished on coloration. The amount of dark pigmentation is greater in the southern subspecies *reticulatus* than in the northern *spatulatus* (Duellman, 1968c, p. 198).

Specimens from Sinaloa are more nearly uniformly colored than are those from Colima and southward. Thirty-two per cent of the specimens from Sinaloa lack dorsal markings, and 45 per cent have small dark flecks on the dorsum, whereas the others have dark dashes or fine reticulations. No specimens from Colima and southward lack dorsal markings; eight per cent of the specimens from Colima have flecks or dashes on the dorsum. The other specimens from Colima and all of those from Michoacán, Guerrero, and Oaxaca have dark reticulations or spots on the dorsum (fig. 301). The color patterns of *T. spatulatus* were assigned values and coded numerically:

- 0—no dorsal markings
- 1—small flecks
- 2—dashes
- 3—fine reticulations
- 4—bold reticulations
- 5—reticulations and spots

All individuals in each of five geographic samples were coded; ranges and means for each sample were calculated (table 59). The sample from Sinaloa (mean color value, 0.96) is distinctly different from the others, which have much higher color values. Specimens from Colima and southward have a mean color value of 3.67.

Taylor (1942) described *Diaglena reticulata* on the basis of one specimen and compared his type with the only two specimens of *Triprion spatulatus* in the United States at that time. In addition to the obvious differences in coloration, he noted that *reticulatus* had a proportionately shorter, broader head, with the canthal ridges uniting farther forward than in *spatulatus* and that the skin was granular on the dorsum, as opposed to smooth in *spatulatus*. The differences in cranial structure apparently are correlated with age and the amount of ossification. Apparent granulation of the skin on the dorsum is due principally to different modes of preservation.

DISTRIBUTION: *Triprion spatulatus* occurs on the Pacific coastal lowlands in central Sinaloa and from Colima to the Isthmus of Tehuantepec, México, and in the Balsas Basin to elevations of about 350 meters (fig. 302).

#### *Triprion spatulatus spatulatus* Günther

*Triprion spatulatus* Günther, 1882, p. 279 [syn-types, B.M.N.H. Nos. 1947.2.25.79-1947.2.25.81 from Presidio de Mazatlán, Sinaloa, México; Alphonso Forrer collector]. Günther, 1901 (1885-1902), p. 293.

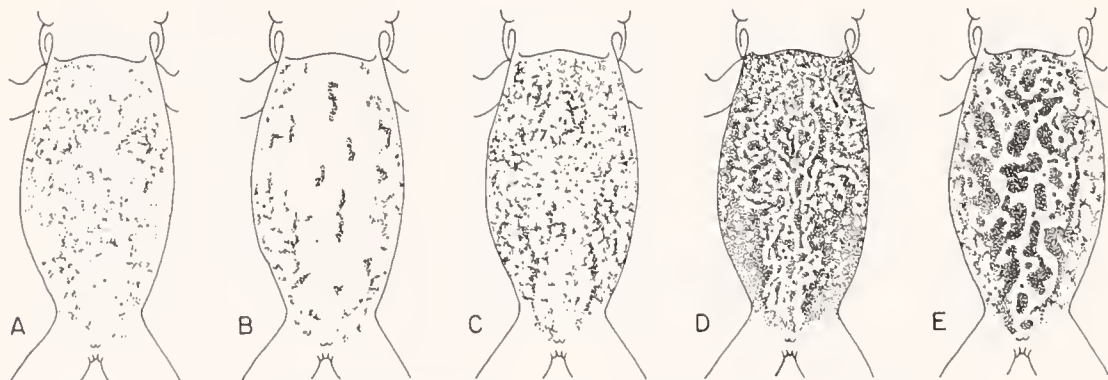


FIG. 301. Diagrammatic representation of dorsal color patterns in *Triprion spatulatus*. A. Value 1, K.U. No. 75275. B. Value 2, U.M.M.Z. No. 115322. C. Value 3, U.M.M.Z. No. 104418. D. Value 4, U.M.M.Z. No. 115321. E. Value 5, K.U. No. 86904. The values are those assigned for coding purposes (table 59); the plain pattern (Value 0) is not shown.

TABLE 59

Geographic Variation in Size and Color Pattern in *Triprrion spatulatus*.  
(Sample Size in First Column for Measurements, in Fourth Column for Color Pattern)

Locality	N	Snout-vent Length		N	Color Pattern
		Males	Females		
Sinaloa	37 ♂, 6 ♀	69.1-85.9 (75.0)	79.6-101.0 (86.1)	105	0-5 (0.96)
Colima	35 ♂, 10 ♀	61.3-74.3 (67.6)	75.4-88.8 (82.2)	323	1-5 (3.58)
Michoacán	5 ♂, 1 ♀	72.0-79.2 (74.8)	83.0	10	3-5 (4.00)
Guerrero	16 ♂, 14 ♀	68.3-80.7 (75.8)	83.1-101.4 (89.3)	30	4-5 (4.26)
Oaxaca	35 ♂, 14 ♀	71.1-87.5 (81.1)	88.6-98.7 (94.4)	49	4-5 (4.28)



FIG. 302. Distribution of the subspecies of *Triprrion spatulatus*.

*Diaglena spatulata*: Cope, 1887, p. 12 [designation of *Triprrion spatulatus* Cünther, 1882, as the type species of *Diaglena* Cope, 1887]. Kellogg, 1932, p. 137. Taylor, 1942b, p. 58. Smith and Taylor, 1948, p. 69.

*Diaglena spatulata spatulata*: Duellman, 1968c, p. 200.

*Triprrion spatulatus spatulatus*: Trueb, 1970a, p. 602 [synonymized *Diaglena* Cope, 1887, with *Triprrion* Cope, 1866a].

**DIAGNOSIS:** This subspecies is distinguished from *T. s. reticulatus* by having a uniformly yellowish tan to dull olive-green dorsum or by having small dark flecks or dashes dorsally. The other subspecies has bold reticulations and/or spots on the dorsum.

**DESCRIPTION:** In a series of 37 males from the vicinity of Villa Unión, Sinaloa, México, the snout-vent length is 69.1 to 85.9 (mean, 75.0) mm.; the ratio of tibia length to snout-vent length is 0.324 to 0.392 (mean, 0.365); the ratio of foot length to snout-vent length is 0.272 to 0.456 (mean, 0.320); the ratio of head length to snout-vent length is 0.304 to 0.386 (mean, 0.353), and the ratio of head width to snout-vent length is 0.171 to 0.261 (mean, 0.218). Six females from the same locality have snout-vent lengths of 79.6 to 101.0 (mean, 86.1) mm. and do not differ significantly from the males in proportions.

The head is moderately small and modified in the form of a bony casque with the skin completely eo-ossified with the skull. The maxillaries and the prenasal are greatly expanded and form a broad labial shelf. The snout protrudes far beyond the leading edge of the lower jaw, and the tip of the snout is pointed and not upturned. The edge of the labial shelf is finely serrate. The nostrils are directed laterally at a point about three-fifths of the distance from the eyes to the tip of the snout. Bony supraorbital and preorbital ridges are present. At their juncture in large females, a bony preorbital knob is developed. A sharp canthal ridge extends anteromedially from the preorbital knob and fuses with its counterpart just posterior to the nasal; from this point a distinct nasal ridge extends anteriorly to the tip of the snout. The loreal region is deeply concave. The labial flange is upturned just anterior to the preorbital ridge; posterior to this point the labial shelf is reduced to a narrow ridge. The eyes are

moderately large, protuberant, and directed anterolaterally. A bony postorbital ridge extends from the orbit to the posterior edge of the skull; the ridge overhangs the upper edge of the tympanum. The posterior edge of the skull is delimited by a low, smooth, transverse bony ridge, which is continuous in all specimens. The bony labial ridge posteriorly obliterates the lower edge of the tympanum in some specimens; likewise, the anterior, down-curved part of the postorbital ridge conceals the anterior edge of the tympanum in some individuals. Consequently, measurements of the tympani are difficult or impossible. The diameter of the tympanum is equal to about half that of the eye.

The upper arms are slender, and the forearms are robust. An axillary membrane and tubercles on the ventrolateral edge of the forearm are absent, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and robust and bear large discs; the diameter of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; none is bifid. The supernumerary tubercles are low, round, and indistinct. A large, flat, elliptical palmar tubercle is present. The prepollex is moderately enlarged and in breeding males is covered with a horny nuptial exerescence which in most individuals extends along the inner edge of the thumb to the base of the disc. Webbing is lacking between the first and second fingers and is rudimentary between the others (fig. 300A). The legs are short; the heels of the adpressed limbs overlap by about one-sixth of the length of the shank. The tibiotarsal articulation extends to the point of the insertion of the arm. A heavy tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately large, flat, and elliptical. The outer metatarsal tubercle is low, round, indistinct, or absent. The toes are moderately long and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are moderately small and subconical; the supernumerary tubercles are small, low, and inconspicuous. The toes are about two-thirds webbed (fig. 300B). The webbing extends from the base of the penultimate phalanx



of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the level of the upper surfaces of the thighs. No anal flap is present, but the area below the anus is covered by moderately large tubercles. The skin is smooth or finely granular on the dorsal surfaces of the body, and somewhat more strongly granular on the flanks and belly. The throat and ventral surfaces of the thighs are weakly granular and the skin on the rest of the venter is smooth. The tongue is ovoid, usually wider anteriorly than posteriorly, shallowly notched behind, and barely free posteriorly. The denticulous processes of the prevomers are small, transverse, narrowly separated, and situated just posteriorly to the posterior margin of the moderately small ovoid choanae. There are four to nine teeth on each process and a total of ten to 16 (mean, 12.0) prevomerine teeth. The vocal slits extend from the posterolateral edge of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and situated posteriorly on the throat.

The general coloration of *Triprion spatulatus spatulatus* is pale green or yellowish tan with green to yellow flecks (pl. 72, fig. 3). The dorsum varies from a pale grayish green to a dull olive-green or yellowish tan. The head is always somewhat darker than the body. The flanks have a yellowish cast even in those individuals which otherwise are olive-green. The venter is white, except for grayish brown flecks on the vocal sac in breeding males. Dark flecks or dashes tend to form indistinct transverse markings on the dorsal surfaces of the thighs and shanks. The iris is dull bronze with black flecks.

The dorsal coloration varies from an absence of dark markings on the body to a pattern of dark brown or black reticulations. The color pattern was noted in 105 specimens; of these 34 lacked markings, 47 had dark flecks on the dorsum, 17 had dark dashes,

six had fine reticulations, and one had bold reticulations (see fig. 301 for a diagrammatic representation of these patterns). In all individuals, the head is more heavily marked than the body; usually the markings on the head consist of short dashes or reticulations.

In preservative the dorsum is grayish brown to creamy tan with or without dull brown markings. The flanks are somewhat lighter. The venter is creamy white, and the vocal sac in breeding males is flecked with grayish brown.

**TADPOLES:** No tadpoles of this subspecies have been collected.

**MATING CALL:** The call of *Triprion spatulatus spatulatus* consists of a single, moderately long, low-pitched note, "braaa." Recordings of a chorus of these frogs contain so much background noise that useful audiospectrograms were impossible to obtain.

**NATURAL HISTORY:** This subspecies inhabits the xeric, thorn-scrub forest on the coastal lowlands of Sinaloa, where it breeds in temporary ponds that are formed in the rainy season, which usually extends from June until early November. On August 14, 1956, I encountered a breeding chorus at a small, temporary pond 31 kilometers north-northwest of Mazatlán, Sinaloa. The frogs were found immediately after a torrential rain; males were calling from bare earth banks at the edge of the pond. Hardy and McDiarmid (1969) reported finding several hundred individuals in a pond at La Cruz, Sinaloa on August 20. They stated that the males were calling in full force and stationed about 35 cm. above the water or on rocks in the water. They observed several amplexing pairs swimming in the water. These authors suggested that although the exact ecological stimulus for breeding is unknown, the combination of sufficient rain, cool weather, and overcast sky may initiate reproductive activity.

**REMARKS:** Duellman and Klaas (1964) reported observations of phragmotactic behavior of this frog in the laboratory. Individuals were observed to back into holes in a log. The hole was too large to be plugged with the head; instead the frogs pressed themselves tightly against the inner wall of the cavity below the hole and slightly flexed the head

so that the labial shelf was flush against the wood.

**ETYMOLOGY:** The specific name is derived from the Latin *spatula*, meaning spoon, and is in reference to the broad labial flanges, which gives the head a spoon shape.

**DISTRIBUTION:** *Triprrion spatulatus spatulatus* inhabits the Pacific coastal lowlands of southern Sinaloa, México (fig. 302).

See Appendix 1 for the locality records of the 127 specimens examined.

***Triprrion spatulatus reticulatus* (Taylor)**

*Diaglena reticulata* Taylor, 1942b, p. 60 [holotype, U.S.N.M. No. 115500 from Cerro Arenal, Oaxaca, México; Thomas MacDougall collector]. Smith and Taylor, 1948, p. 69.

*Diaglena spatulata reticulata*: Duellman, 1968c, p. 200.

*Triprrion spatulatus reticulatus*: Trueb, 1970a, p. 602 [synonymized *Diaglena* Cope, 1887, with *Triprrion* Cope, 1866a].

**DIAGNOSIS:** This subspecies is distinguished from the nominate subspecies by having bold dark brown or black reticulations, and in some individuals spots also, on a yellowish tan to olive-green dorsum. The nominate subspecies lacks dark dorsal markings or has only small dark flecks or dashes.

**DESCRIPTION:** Males of this subspecies attain a maximum snout-vent length of 80.7 mm., and females reach 101.4 mm. In a series of 16 males from El Zapote, Guerrero, México, the snout-vent length is 68.3 to 80.7 (mean, 75.8) mm.; the ratio of tibia length to snout-vent length is 0.372 to 0.417 (mean, 0.393); the ratio of foot length to snout-vent length is 0.326 to 0.360 (mean, 0.345); the ratio of head length to snout-vent length is 0.343 to 0.379 (mean, 0.360), and the ratio of head width to snout-vent length is 0.201 to 0.248 (mean, 0.233). Fourteen females from the same locality have snout-vent lengths of 83.1 to 101.4 (mean, 89.3) mm. and do not differ from the males significantly in proportions. There is a geographic trend from north (Colima) to south (Oaxaca), in snout-vent lengths; both males and females from Oaxaca are noticeably larger than are those from Colima (table 59).

Structurally this subspecies is like the nominate subspecies, except that the edge of the labial flange tends to be slightly more

serrate, and the fusion of the canthal ridges in large specimens is at a point between the nostrils, farther anteriorly than in the nominate subspecies. The number of prevomerine teeth on each process in *reticulatus* is five to eight, and a total number of prevomerine teeth is 11 to 16 (mean, 13.6).

The general coloration of *Triprrion spatulatus reticulatus* is pale yellowish tan or pale olive-green with dark brown or black reticulations and spots on the dorsum (pl. 72, fig. 2). At night individuals from Tehuantepec, Oaxaca, México, had a pale yellowish green dorsum fading to yellow on the flanks. The head was olive-brown. The dorsal reticulations were dark brown, and the venter, including the vocal sac was white. The iris was pale gold flecked with black. Specimens from El Zapote, Guerrero, México, tended to be more greenish tan with dark brown reticulations.

Some specimens from the northern part of the range (Colima) have dark markings consisting of dashes or flecks, and approximately one-third of the specimens have rather fine reticulations on the back. The other specimens from Colima and all of those from farther south have a dorsal pattern consisting of bold reticulations or of reticulations and spots (see fig. 301 for examples of these color patterns). A slight, but continual, cline exists for an increase in the amount of dark pigmentation on the dorsum from north to south (table 59).

In preservative the dorsum is creamy tan to pale grayish brown with dark brown or black markings. The markings on the dorsal surfaces of the limbs tend to form bold reticulations rather than transverse bands. The venter is uniformly creamy white.

**TADPOLES:** The only available tadpoles are recent hatchlings that are unsuitable for a diagnostic description.

**MATING CALL:** The call of *Triprrion spatulatus reticulatus* consists of a single, low-pitched note "braaa." The note repetition rate varies from 10 to 17 (mean, 13.1) notes per minute; individual notes have a duration of 0.76 to 0.93 (mean, 0.85) of a second. The pulse rate is 88 to 114 (mean, 99.0) pulses per second. The fundamental frequency varies from 89 to 134 (mean, 103) cycles per

second, and the dominant frequency varies from 1589 to 1869 (mean, 1745) cycles per second. There are no definitely emphasized harmonics above the dominant frequency (pl. 34, fig. 2).

**NATURAL HISTORY:** This subspecies inhabits tropical scrub forests where the rainy season is restricted to the months of June to September. Peters (1955) found a breeding chorus at Ostula, Michoacán, on July 14, 1950; I found the species breeding near Tehuantepec, Oaxaca, on July 5, 1956, near Salina Cruz, Oaxaca, on July 6, 1958, and near El Zapote, Guerrero, on June 12, 1964. In each instance, heavy rains preceded the congregation of the frogs at the breeding sites. At the localities in Oaxaca, males were calling from bare mud or gravel banks near temporary ponds, although a few males called from distances of three meters from the water. At El Zapote, Guerrero, some males were observed calling from shallow water at the edge of the pond, but most were calling from barren ground near the ponds and up to distances of 10 meters from the water. Several amplexant pairs have been observed on land, but none has been seen in the water.

Taylor (1942b) reported that the type specimen of *reticulatus* was found in a bromeliad. Another specimen from near Tehuantepec was found inside a rotting log.

**REMARKS:** The minor differences in size and structure between *Triprrion spatulatus* as known in Sinaloa, and those populations to the south, previously referred to the species *reticulatus* do not seem to be taxonomically significant. The major differences between northern and southern populations are in the color pattern. Although genetic interchange between the populations herein referred to *reticulatus* and the northern *spatulatus* can not be demonstrated at this time, the two populations are considered to be subspecifically related, because of their general structure similarities and because of my desire to emphasize the similarities, rather than to place the two populations on a status equal to that accorded to *petasatus* and the species *spatulatus*.

**ETYMOLOGY:** The specific name is Latin, meaning made like a net, and refers to the dorsal coloration.

**DISTRIBUTION:** *Triprrion spatulatus reticulatus* inhabits coastal lowlands of low foothills to elevations to about 350 meters from Colima southeastward to the Isthmus of Tehuantepec, Oaxaca, México; this species also occurs in the Balsas Basin in Michoacán (fig. 302).

See Appendix 1 for the locality records of the 432 specimens examined.

### *Triprrion petasatus* (Cope)

*Pharyngodon petasatus* Cope, 1865b, p. 193 [holotype, U.S.N.M. No. 12287 from Cenote Tamaché (17 kilometers north of Mérida, Yucatán, México; Arthur Schott collector)].

*Triprrion petasatus* Cope, 1866a, p. 127. Boulenger, 1882a, p. 431. Günther, 1901 (1885-1902), p. 293. Kellogg, 1932, p. 138. Smith and Taylor, 1948, p. 70. Stuart, 1963, p. 42. Trueb, 1970a, p. 602.

**DIAGNOSIS:** This is a moderately large species (males to 60.8 mm.; females to 74.2 mm.) that is readily distinguished from other Middle American casque-headed hylids by having a large, upturned prenasal, which with the expanded maxillaries forms a broad labial shelf. Furthermore, *petasatus* has a large dermal sphenethmoid, paired vocal sac, and lacks odontoids on the palatines. *Triprrion spatulatus* has a single, median vocal sac, odontoids on the palatines, a prenasal that is not upturned, and no dermal sphenethmoid. *Pternohyla* has only moderate labial flanges and lacks a dermal sphenethmoid and prenasal. Furthermore, *Pternohyla* is squat and toad-like in appearance and has a large spade-like inner metatarsal tubercle. *Anotheca* lacks labial flanges and has spines on the supratympanic and occipital ridges.

**DESCRIPTION:** Males attain a maximum snout-vent length of 60.8 mm., and females reach 74.2 mm. In a series of 20 males from Chichén Itzá, Yucatán, México, the snout-vent length is 48.1 to 60.8 (mean, 54.6) mm.; the ratio of tibia length to snout-vent length is 0.374 to 0.414 (mean, 0.393); the ratio of foot length to snout-vent length is 0.305 to 0.351 (mean, 0.332); the ratio of head length to snout-vent length is 0.650 to 0.742 (mean, 0.694); the ratio of head width to snout-vent length is 0.255 to 0.302 (mean, 0.274), and the ratio of the diameter of the tympanum to that of the eye is 0.473 to 0.605 (mean, 0.548). The ten females from the same locality have snout-vent lengths of 65.0 to 75.2 (mean, 70.7) mm. and show no significant differences



in proportions from the males. Specimens from the southern part of the range (La Libertad, El Petén, Guatemala) are smaller (mean snout-vent length in 20 males, 52.1 mm.) and have proportionately longer legs and smaller heads (see Duellman and Klaas, 1964, p. 312).

The head is large and modified in the form of a bony casque with the skin completely co-ossified with the skull (fig. 298). The maxillaries and the prenasal are greatly expanded and form a broad labial shelf. The snout protrudes far beyond the leading edge of the lower jaw, and the tip of the snout is upturned. The edge of the labial shelf is serrate. The nostrils are directed dorsally at a point about two-thirds of the distance from the eyes to the tip of the snout. A bony pre-orbital knob is present at the anterior edge of the orbit; in some individuals, especially large females, the knob is greatly enlarged so as to overhang the anterior edge of the orbit. A sharp canthal ridge extends from the preorbital knob to a point just posterior to the nostril. From the point of confluence of the canthal ridges a low bony ridge extends anteriorly between the nostrils to the tip of the snout. The loreal region is deeply concave. A bony preorbital ridge forms the anterior border of the orbit and extends ventrally from the preorbital knob to the labial flange, which is narrow posterior to the preorbital ridge. The eyes are large, protuberant, and directed anterolaterally. A bony supratympanic ridge extends from the posterior edge of the orbit to the posterior edge of the skull; the ridge overhangs the upper edge of the tympanum, which otherwise is distinct. The posterior edge of the skull is delimited by a finely serrate transverse bony ridge, which is continuous in some specimens, but notched medially in most individuals.

The upper arms are slender, and the forearms are robust. An axillary membrane and tubercles on the ventrolateral edge of the forearm are absent, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately long and robust and bear large discs; the diameter of that on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are large and round; none is bifid. The super-

numerary tubercles are moderately large and round. A large, flat palmar tubercle is present. The prepollex is moderately enlarged and in breeding males is covered with a horny nuptial excrecence, which in most individuals extends along the inner edge of the thumb to the disc. Webbing is lacking between the first and second fingers and is rudimentary between the others (fig. 300C). The legs are short; the adpressed heels barely overlap. The tibiotarsal articulation extends to the posterior edge of the tympanum. A well-defined tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, flat, and elliptical; the outer metatarsal tubercle is minute and round. The toes are long and bear discs that are slightly smaller than those on the fingers. The sub-articular tubercles are round and somewhat larger than the small, round supernumerary tubercles. The toes are about two-thirds webbed (fig. 300D). The webbing connects the first and second toes at the bases of the penultimate phalanges and extends from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. No anal flap is present, but a dermal fold extends postero-ventrally from a point on either side of the anal opening. The skin is smooth on the dorsum (except head), chin, and ventral surfaces of the limbs (except thighs); it is granular on the flanks, belly, and ventral surfaces of the limbs. The tongue is round, slightly wider in front than behind, and barely free posteriorly; it is shallowly notched posteriorly in most individuals and marginate in some specimens. In most specimens the dentigerous processes of the prevomers are transverse or slightly curved, whereas in some specimens the processes are inclined posteromedially. The processes lie between the moderately large ovoid or longitudinally elliptical choanae. Males have a total of 8 to 15 (mean, 11.6) prevomerine teeth, and females have 14 to 20 (mean, 16.1). The vocal slits extend from the posterolateral edge of the tongue

to the angles of the jaws. The vocal sac is subgular, paired, and situated posteriorly on the throat.

The general coloration of *Triprion petasatus* is olive-green or tan with dark brown or black markings on the dorsum (pl. 72, fig. 1). In most males the dorsum is olive-green with dark brown or black irregularly shaped blotches, spots, or numerous flecks on the back. The dorsal surfaces of the limbs are colored like the body and have distinct dark brown or black transverse bands on the shanks and forelimbs; the bands are indistinct or lacking on the thighs and the feet in some specimens. The flanks are olive-green or yellowish green. Most females are pale tan, and some are olive-brown; all have dark brown or black markings. In specimens of both sexes the posterior surfaces of the thighs are dark brown or reddish brown, and the anterior surfaces are pale brown. The head is colored like the body but lacks dark markings. In some individuals silvery gray flecks are present on the dorsum; these are most apparent on the head. The belly is white, and the ventral surfaces of the shanks and feet are tan. In breeding males the vocal sac is yellow with brown flecks. The iris is golden bronze with fine black reticulations.

In preservative the dorsum varies from grayish tan to olive-brown with dark brown markings. Small white flecks are present on the dorsal surfaces of the head, body, and limbs in some individuals. A few specimens lack dorsal markings. The posterior surfaces of the thighs are dark brown, and the anterior surfaces are pale brown. The ventral surfaces of the forearms and thighs are creamy tan and those of the shanks and feet are brown. The throat and belly are creamy white with some brown pigment posterolaterally on the throat in some females and in most males;

in the other males the entire throat is brown.

**TADPOLES:** The embryonic and larval development were described in detail by Duellman and Klaas (1964), who noted that the oral suckers persisted into developmental stage 24 and that the teeth were not fully developed until stage 30. Measurements of the tadpoles showed that there is a gradual increase in the length of the tail relative to body length through stage 41. Duellman and Klaas (1964) noted that a great variation in size occurred in developmental stage 25 and suggested that the rate of growth is more rapid in that stage or that the duration of the stage is longer than that of other stages. Throughout development the head and body become darker; the amount of pigment increases in the ventral fin, and the pattern of pigmentation of the fins changes from flecks to reticulation and finally to venation.

A typical tadpole in developmental stage 30 has a body length of 12.3 mm. and a total length of 27.0 mm. The body is ovoid and slightly wider than deep. In dorsal profile the snout is bluntly rounded and in lateral profile acutely rounded. The nostrils are dorsal in position about two-thirds of the distance from the eyes to the tip of the snout and directed dorsolaterally. The eyes are moderately small and dorsolateral. The long, sinistral spiracle has its opening just below the midline at a point about midlength on the body. The anal tube is short and dextral. The tail is moderately deep and pointed terminally. The caudal musculature is moderately heavy and does not extend to the tip of the tail. At the midlength of the tail the depth of the musculature is equal to the depth of either fin. The dorsal fin extends onto the body and is deepest at midlength of the tail; the ventral fin is deepest at about one-third of the length of the tail (fig. 303).

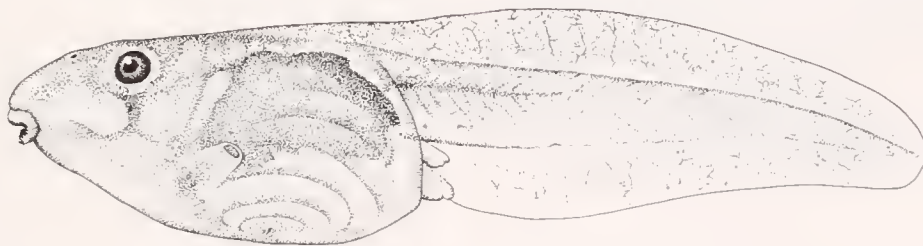


FIG. 303. Tadpole of *Triprion petasatus*, K.U. No. 71731.  $\times 4$ .

In life the tadpoles are dull grayish brown with creamy tan caudal musculature and transparent fins with brown reticulations; the iris is pale bronze. In preservative the dorsum is dark brown, and the venter is pale brown. The caudal musculature is creamy gray. The ventral fin lacks pigment, and the dorsal fin is venated.

The mouth is moderately small and antero-ventral. Lateral folds and a shallow ventral fold are present in the lips, which are bordered by one row of small papillae, except on the median part of the upper lip, which is bare. Small papillae are present in the lateral folds. The beaks are moderately heavy and bear small, pointed serrations. The upper beak is in the form of a high arch and has long, slender lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are about equal in length, and the second lower row is narrowly interrupted medially. The lower rows are complete; the first lower row is nearly as long as the upper rows, and the other lower rows are progressively shorter (fig. 304).

In tadpoles in developmental stage 34 the eanthal ridges are apparent, and those in stage 41 have a weak occipital ridge. In stage 45 the tadpoles have obvious eanthal and occipital ridges and have an acutely angular snout that projects well beyond the leading edge of the lower jaw.

**MATING CALL:** The call of *Triprrion petasatus* consists of a single, low-pitched note. The notes are quickly repeated, so that the call sounds like the quacking of a duck. The

frogs normally produce 33 to 54 (mean, 41) notes in succession. The note repetition rate is 45 to 52 (mean, 48.7) notes per minute. Each note has a duration of 0.26 to 0.39 (mean, 0.30) of a second and a pulse rate of 80 to 90 (mean, 84.7) pulses per second. The fundamental frequency varies from 210 to 350 (mean, 287) cycles per second, and the dominant frequency varies from 1900 to 2450 (mean, 2096) cycles per second. Usually five harmonics above the dominant frequency are emphasized with decreasing force from the lowest to the highest (pl. 34, fig. 3).

**NATURAL HISTORY:** The following account is excerpted from Duellman and Klaas (1964, pp. 312-315); the reader is referred to their account for more details on habitat and life history. *Triprrion petasatus* inhabits low, xerophilous forest or savannas in areas characterized by shallow soils and a low amount of rainfall that is highly seasonal in distribution.

Breeding activity follows rains which provide water in solution pits, sink holes, and *aguadas*. Stuart (1935, p. 37) found the species breeding in an intermittent *aguada* at La Libertad, El Petén, Guatemala between May 23 and 30, 1933. My own observations on breeding activity of *Triprrion petasatus* were made in July, the month in which most other persons have observed the species (Gaige, 1936, p. 290, and Maslin, 1963, p. 3).

On July 22, 1962, *T. petasatus* was breeding at localities 9 and 12 kilometers east of Chichén Itzá, Yucatán, México. At the first locality males were calling from branches of low trees and bushes around two small solution basins. At the latter locality males and clasping pairs were on the ground at the edge of a water-filled earthen pit. On the same night a large breeding congregation was found at a locality 3.5 kilometers east of Yokdzonot, Yucatán, where males were calling from branches of dense trees and bushes around a small solution pit; amplexing pairs were on branches to heights of 2.5 meters above the ground. Because most calling males and many clasping pairs were observed in trees, probably the frogs spend the days and the dry season in trees. Stuart (1935, p. 37) found individuals in holes in trees around an *aguada* in which the species was breeding at La Libertad, Guatemala. Stuart observed that

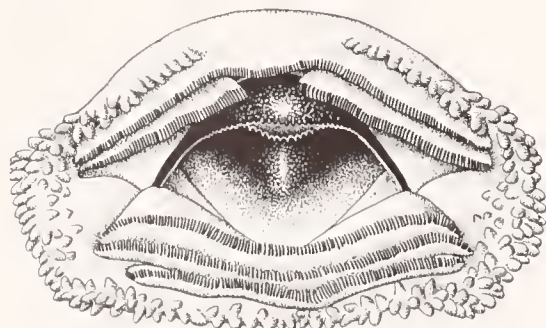


FIG. 304. Mouth of tadpole of *Triprrion petasatus*, K.U. No. 71731.  $\times 25$ .



the frogs plugged the cavities in trees with their heads.

Eggs are deposited in clumps in the water; in Yucatán eggs were found in shallow basins or solution pits. Tadpoles congregate in shaded areas and seek refuge in the decaying vegetation on the bottom of the basin or pit.

Four recently metamorphosed young have snout-vent lengths of 15.5 to 16.1 (mean, 15.8) mm. These specimens have a protruding snout and slightly flared lips.

REMARKS: The developmental and internal cranial osteology of this species has been studied in detail (Trueb, 1970a).

ETYMOLOGY: The specific name *petasatus* is Latin meaning with a hat on and refers to the helmet-like casque.

DISTRIBUTION: *Triprion petasatus* occurs in the lowlands of the Yucatan Peninsula, southward in subhumid habitats to the savannas of central El Petén, Guatemala (fig. 305).

See Appendix 1 for the locality records of the 273 specimens examined.

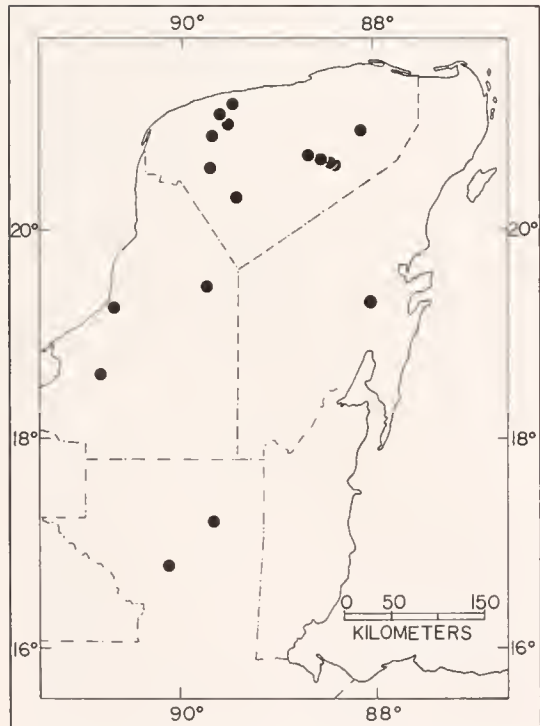


FIG. 305. Distribution of *Triprion petasatus*.

### Genus *Pseudacris* Fitzinger

*Pseudacris* Fitzinger, 1843, p. 31 [type species, *Rana nigrita* LeConte, 1824, by monotypy].

*Chorophilus* Baird, 1854, p. 59 [type species, *Rana nigrita* LeConte, 1825, by original designation].

*Helocaetes* Baird, 1854, p. 59 [type species, *Hyla triseriata* Wied, 1839, by subsequent designation (Schmidt, 1953)].

GENEROTYPE: The first usage of the name *Pseudacris* was in a subgeneric position under *Acris* by Fitzinger (1843, p. 31): "*Pseudacris* . . . Am. . . . *Acr. nigrita* Dum. Bibr." Duméril and Bibron (1841, p. 509) used the combination *Acris nigrita* for the frog originally named *Rana nigrita* by LeConte (1825, p. 282). Since Fitzinger associated no other species with *Pseudacris*, *Rana nigrita* LeConte is the type species by monotypy.

ETYMOLOGY: The generic name is derived from the Greek *pseudes*, meaning false, and the Greek *akris*, in this case referring to the genus *Acris*.

DEFINITION: The frogs in this genus are small pond-breeding species; males attain snout-vent lengths of 41 mm. and females, 46 mm. The dorsum is tan, gray, or green with darker stripes or spots arranged in longitudinal series. All have a dark line from the nostril to the eye; the line is expanded posterior to the eye and in some species continues to the groin. In most species, a pale labial stripe is present. The webbing is vestigial on the hand, and the toes are less than one-third webbed. The discs are barely wider than the digits. A tarsal fold is absent, and dermal appendages on the limbs and an axillary membrane are lacking. The skin is smooth dorsally and not involved in co-ossification with the skull. Males have a single, median, subgular vocal sac but lack horny nuptial excrescences. The skull is weakly ossified and has a large frontoparietal fontanelle (fig. 306). The sphenethmoid is ossified anteriorly between the nasals to the end of the septum nasi. The nasal is moderately long and at least partially in bony contact with the sphenethmoid. The squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends only about one-third of the distance to the maxillary. The columella is expanded distally. The quadratojugal is present and articulates with

the maxillary. The prevomer is poorly ossified and the palatine is weak. The medial ramus of the pterygoid does not articulate with the prootic. Teeth are present on the premaxillaries, maxillaries, and prevomers. The tadpoles have deep fins and small anteroventral mouths with two upper and three lower rows of teeth. The mating calls consist of a series of quickly repeated notes, which in some species are so closely spaced that the call sounds like a trill. The chromosome numbers are  $n=12$ ,  $2n=24$  (known only in *P. brachyphona* and *triseriata*).

**COMPOSITION OF GENUS:** Seven species are included in the genus; three of these are polyploid. Only one species, *Pseudacris clarkii* occurs in Middle America, and two Mexican specimens of that species have been examined.

**DISTRIBUTION:** North America westward to the Rocky Mountains, northward to Hudson Bay and northwestern Canada and southward to the Gulf of Mexico. In Middle America, the genus occurs only in the lower Rio Grande Valley.

**DISCUSSION:** The frogs of the genus *Pseudacris* differ from most North and Middle American *Hyla* by having small discs and greatly reduced webbing on the feet. No other external features will distinguish them from *Hyla*. If these frogs occurred in South America, they probably would not have been recognized generically.

*Pseudacris* seems to be more closely related to the *Hyla eximia* group than to any other groups of *Hyla* or to *Acris*. *Pseudacris* differs from members of the *Hyla eximia* group by having a more extensively ossified sphenethmoid and better developed nasals which are in contact with the sphenethmoid. Thus, by comparison with *Pseudacris*, the skulls of *Hyla eximia* and its allies are reduced, whereas the webbing of the feet and the sizes of the discs are reduced in *Pseudacris* as compared with *Hyla eximia*.

The morphological similarities of the adults and tadpoles, the likeness of breeding habits, the general structural similarities of the mating calls, and the nearly complementary geographic ranges of *Pseudacris* and the *Hyla eximia* group strongly suggest close phyletic relationships between the groups. Possi-

bly they both descended from a widespread Nearectic prototype, which gave rise to *Pseudacris*, in eastern North America and to the *Hyla eximia* group in western North America.

A discussion of the intrageneric relationships of *Pseudacris* is inappropriate here. The various species have been reviewed by Schwartz (1957) and Smith and Smith (1952), and experimental evidence on reproductive isolating mechanisms was summarized by Meeham (1965).

### *Pseudacris clarkii* (Baird)

*Helocates clarkii* Baird, 1854, p. 60 [syntypes, U.S.N.M. No. 3313 (*vide* Cochran, 1961, p. 50),<sup>15</sup> from Galveston, Galveston County, Texas; M. Dean collector].

*Chorophilus triseriatus clarkii*: Cope, 1875, p. 30.

*Pseudacris triseriata clarkii*: Burt, 1932, p. 80.

*Pseudacris clarkii*: Smith, 1934, p. 462.

**DIAGNOSIS:** This small, slender species with a subaeuminate snout has a dorsal pattern of irregular dark green to reddish brown spots on a pale green, tan or gray ground color; a pale labial stripe is present; a dark interorbital triangular mark, not bordered by white usually is present. This color pattern, in combination with smooth skin, toes less than one-third webbed, and barely enlarged terminal discs on the digits distinguishes *Pseudacris clarkii* from other hylids. The only other small hylids in México with a triangular interorbital mark are *Acris crepitans*, *Hyla regilla*, and *Hyla staufferi*. The former has the interorbital mark usually bordered by white, tubercular dorsal skin, and much more webbing on the feet. *Hyla staufferi* and *Hyla regilla* have a linear pattern on the dorsum, more webbing on the feet, and larger discs than *Pseudacris clarkii*.

**DESCRIPTION:** Males of this species attain a maximum snout-vent length of 29 mm., and

<sup>15</sup> Baird (1854, p. 60) did not designate type specimens but stated that the habitat was "Galveston and Indianola, Texas." Yarrow (1882, p. 170) listed only U.S.N.M. No. 3313 under "*Chlorophilus triseriatus clarkii*." Cope (1889, p. 347) listed the same specimen, plus U.S.N.M. No. 3317 from Indianola and U.S.N.M. No. 3315 from between Indianola and San Antonio, Texas; both were collected by John H. Clark and presumably along with U.S.N.M. No. 3313 formed the type series for Baird's description of *Helocates clarkii*.

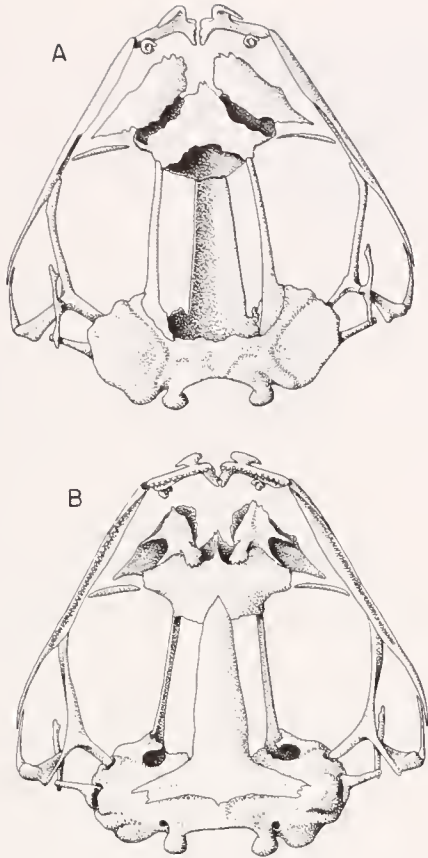


FIG. 306. Dorsal (A) and ventral (B) views of the skull of *Pseudacris clarkii*, K.U. No. 60373.  $\times 6$ .

females reach 31 mm. The two known specimens from México are juveniles having snout-vent lengths of 15 and 18 mm.

The head is narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acuminate, in lateral profile, it is acuminate and projects beyond the margins of the lips. The snout is long, and slightly protuberant nostrils are situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is round, and the loreal region is barely concave; the lips are moderately thick and not flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is absent. There are no rows of tubercles on the ventrolateral edge of the forearm, but a distinct dermal fold is present on the wrist. The fingers are long and slender and bear discs that are only slightly wider than the fingers. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are moderately large and round. A large quadrangular palmar tubercle is present. The prepollex is slightly enlarged and in breeding males does not bear a nuptial excrescence. The webbing on the hand is vestigial (fig. 307A). The legs are short and robust; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the tympanum. A distinct transverse dermal fold is present on the heel, and a well-developed, flap-like tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, elliptical, and elevated. A conical outer metatarsal tubercle is present. The toes are long and slender and bear very small discs; the subarticular tubercles are large and round, whereas the supernumerary tubercles are barely evident only on the proximal segments of each digit. The toes are webbed only basally (fig. 307B).

The anal opening is directed posteriorly near the upper level of the thighs; a short, broad anal sheath is present. The skin on the dorsum is weakly granular, whereas that on the venter is strongly granular. The tongue is cordiform, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are small rounded elevations that are widely separated medially and lie between the ovoid choanae. Usually there are only two or three teeth on each elevation. The vocal slits extend from the mid-lateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Pseudacris clarkii* is pale green or olive-green above with elongate brown spots usually forming three rows on the back (pl. 64, fig. 4). The dorsal surface varies from pale gray to green to dull olive-gray. The spots on the back and transverse bars on the limbs vary from brown to dark olive-green. There is a dark brown



stripe from the nostril, to the eye, and onto the anterior part of the flank. A narrow cream labial stripe is present. The venter is creamy white. The iris is pale bronze with black flecks. In preservative, the dorsum varies from pale tan to grayish brown; the dorsal markings are to dark brown, and the venter is creamy tan.

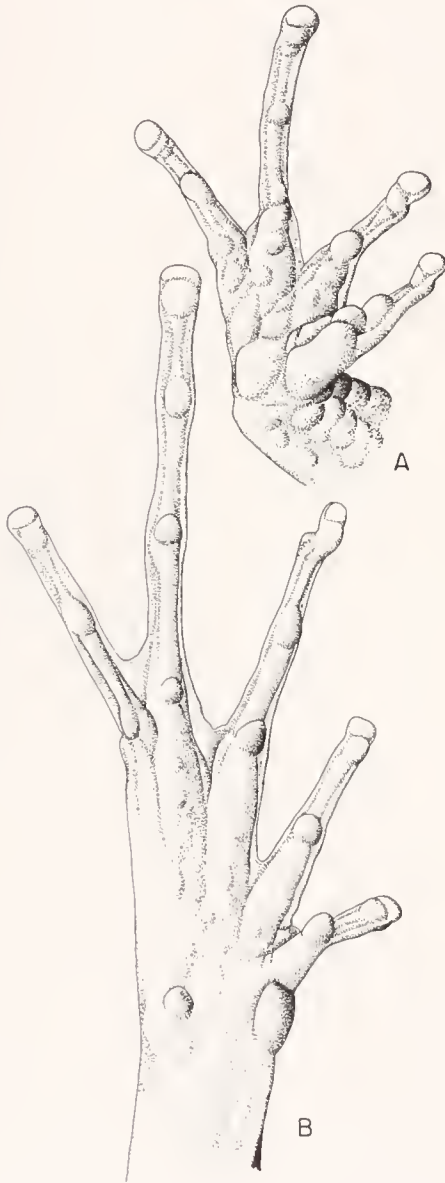


FIG. 307. Hand (A) and foot (B) of *Pseudacris clarkii*, K.U. No. 110232.  $\times 8$ .

**TADPOLES:** No tadpoles of this species are available from Middle America; the following description is based on individuals from Arlington, Texas, provided by William F. Pyburn. A typical tadpole in developmental stage 33 has a body length of 8.8 mm. and a total length of 23.0 mm. The body is deeper than wide; in dorsal profile the snout is bluntly rounded, and in lateral profile it is round. The eyes are small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The spiracle is directed posteriorly at a point below the midline and about three-fifths of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is slender and extends to the tip of the pointed tail. The caudal fins are deep; at midlength of the tail the depth of either fin is half again the depth of the caudal musculature. The dorsal fin extends onto the body (fig. 308).

In preservative the tadpoles are dark brown or nearly black above, and the venter is transparent. The caudal musculature is pale creamy tan below and dark brown above. The caudal fins are transparent and marked by a few small black flecks.

The mouth is moderately small and situated anteroventrally. The median part of the upper lip is bare; elsewhere the lips are bordered by one or two rows of small papillae. The beaks are slender and bear short, pointed serrations. The upper beak is very broad and has a short, blunt lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are much longer than the lower ones, and the second upper row is broadly interrupted medially. The first and second lower rows are much longer than the third lower row, and the first lower row is narrowly interrupted medially in some specimens (fig. 309).

**MATING CALL:** The mating call of *Pseudacris clarkii* consists of a series of quickly repeated, low-pitched notes. Analysis of the calls of four individuals from Montgomery County, Kansas, indicates the call rate is 130 to 160 (mean, 144) notes per minute. The duration of the note varies from 0.15 to 0.18 (mean, 0.17) of a second, and the notes have

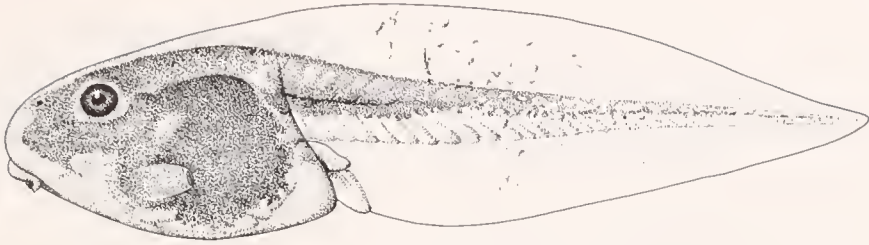


FIG. 308. Tadpole of *Pseudacris clarkii*, K.U. No. 116932.  $\times 5$ .

90 to 97 (mean, 93) pulses per second. The fundamental frequency varies from 74 to 83 (mean, 78) cycles per second, and the dominant frequency varies from 2508 to 2652 (mean, 2554) cycles per second (pl. 37, fig. 1).

**NATURAL HISTORY:** *Pseudacris clarkii* inhabits prairie and subhumid scrub land. The species breeds at the time of the spring rains between early March and late June. Males call from clumps of grass in shallow water. The tadpoles develop in shallow grassy ponds.

**REMARKS:** *Pseudacris clarkii* is known from México on the basis of two specimens (S.U. Nos. 15449 and 15450) from 8 kilometers west of Matamoros, Tamaulipas (Lynch, 1965a, p. 31).

**ETYMOLOGY:** The specific name is a patronym for John H. Clark, the collector of the type specimen.

**DISTRIBUTION:** *Pseudacris clarkii* occurs in the central United States from south-central Kansas to the Gulf of Mexico; the species is known in México only from the lower Rio Grande Valley in Tamaulipas (fig. 310).

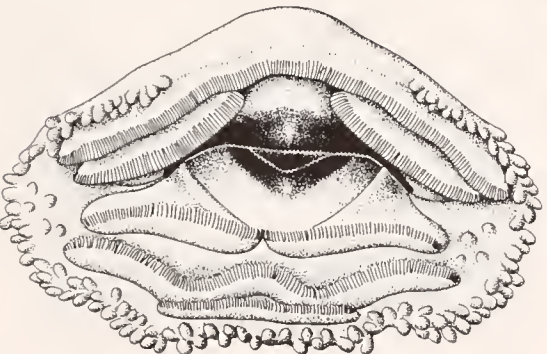


FIG. 309. Mouth of tadpole of *Pseudacris clarkii*, K.U. No. 116932.  $\times 30$ .

See Appendix 1 for the locality records of the two specimens examined.

### Genus *Acris* Duméril and Bibron

*Acris* Duméril and Bibron, 1841, 1. 506 [type species *Rana gryllus* LeConte, 1825, by fiat].

**GENEROTYPE:** Duméril and Bibron (1841) included *Rana gryllus* LeConte, 1825, and *Rana nigrita* LeConte, 1825. Neither was designated as the type of the genus, although *gryllus* was listed first (page 507; *nigrita* was treated on page 509). Fitzinger (1843, p. 31) proposed the following arrangement:

"1. Gen. *Acris*. Dum. Bibr.

*Pseudacris* . . . Am. . . . *Acr. nigrita*.  
Dum. Bibr.

*Acris* . . . Am. . . . *Acr. gryllus*. Dum.  
Bibr."

hus, by selecting *nigrita* (one of the two

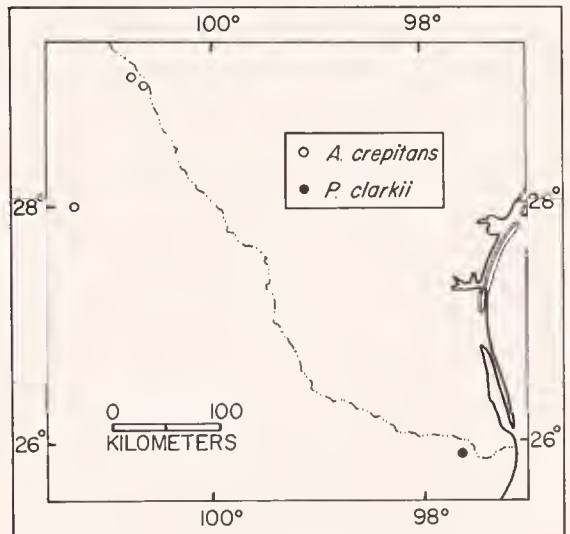


FIG. 310. Distribution of *Pseudacris clarkii* and *Acris crepitans* in México.

species included in *Acris* by Duméril and Bibron) as the type species of the genus *Pseudacris* Fitzinger, by fiat restricted *gryllus* to *Acris*.

**ETYMOLOGY:** Duméril and Bibron (1841, p. 506) noted that the generic name was Greek, "Akpis, l'un des noms de la Sauterelle." Thus, the generic name is a name for a grasshopper and is appropriately applied to these frogs capable of prodigious leaps.

**DEFINITION:** Members of this genus are small pond-breeding species; males attain snout-vent lengths of 29 mm. and females 34 mm. The dorsum is pale brown or gray usually with a dark interorbital triangular mark and with or without a green or rusty tan middorsal patch. A prominent longitudinal black bar is present on the posterior surfaces of the thighs. The webbing is vestigial on the hand, and the toes are about three-fourths webbed; the terminal phalanges are not expanded. A tarsal fold is present and dermal appendages on the limbs and an axillary membrane is lacking. The skin on the dorsum is tubercular and not involved in integumentary-cranial co-ossification. Males have a single, median, subgular vocal sac and lack horny nuptial excrescences. The skull is weakly ossified and has a large frontoparietal fontanelle (fig. 311). The sphenethmoid is greatly reduced. The nasals are small and widely separated medially; they are not in contact with the sphenethmoid or maxillaries. The squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends only about half of the distance to the maxillary. The quadratojugal is present and in contact with the maxillary. The prevomers are greatly reduced and do not articulate with the maxillaries or premaxillaries. The palatine is slender and not in bony contact with either the maxillary or the sphenethmoid. The medial ramus of the pterygoid is not in bony contact with the prootic. Teeth are present on the premaxillaries, maxillaries, and prevomers. The tadpoles have moderately deep fins and small anteroventral mouths with two upper and two lower tooth rows. The mating call consists of a long series of short eliciting notes. The chromosome numbers are  $n=11$ ,  $2n=22$  (Cole, 1966).

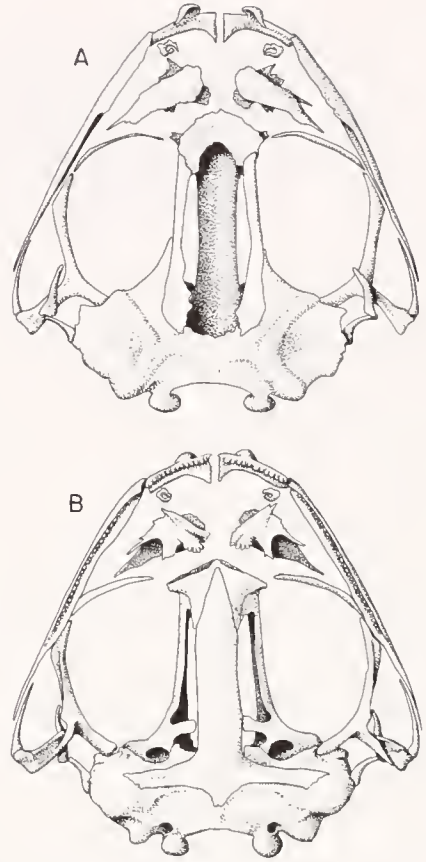


FIG. 311. Dorsal (A) and ventral (B) views of the skull of *Acris crepitans*, K.U. No. 59952.  $\times 6$ .

**COMPOSITION OF GENUS:** Two species (*A. crepitans* and *A. gryllus*) are generally recognized, although some previous workers have suggested that these two species intergrade. Two subspecies usually are recognized in *gryllus*, whereas the status of subspecies (*blanchardi* and *paludicola*) of *crepitans* is in question. Only *crepitans* occurs in Middle America, and I have examined 33 preserved frogs from México.

**DISTRIBUTION:** The genus occurs throughout eastern United States from New York and Michigan to South Dakota and eastern Colorado and southward in isolated populations through eastern New Mexico and western Texas to Coahuila, México.

**DISCUSSION:** The frogs of the genus *Acris* are distinctive among the hylids in a number of morphological and behavioral features. They are non-arboreal, aquatic-margin spe-



cies and thus fill the ecological position of a small *Rana*. The frogs are active and call by day, as well as at night. The eggs are deposited singly or in small groups adherent to aquatic vegetation. In the tadpoles, the entire upper lip is devoid of papillae, and the eyes are dorsal; in each of these characters, the tadpoles are like those of most North American *Rana*. The presence of long toes, no expanded digits, and a considerable amount of webbing are obvious adaptations for their semi-aquatic habits. The smooth skin on the throat and chest is unusual for a hylid and is more like the condition in *Rana*. The skull of *Acris* is so greatly reduced that the usefulness of cranial characters is restricted. Chantell (1968) noted the distinctiveness of *Acris* among North American hylids and suggested that it possibly was most closely related to *Limnaeodius*, which obviously is a hylid with reduced cranial elements. Studies of chromosomes (Duellman and Cole, 1965; Cole, 1966; Duellman, 1967b) have shown that *Acris* is unique among Holarctic and Neotropical hylids by having chromosome numbers of  $n=11$ ,  $2n=22$ ; this number is common in Australian species of *Hyla* (Straughan, pers. comm.). Most hylids have  $n=12$ ,  $2n=24$ , but some groups have haploid numbers of 13, 14, or 15 and diploid numbers of 26, 28, and 30. All ranids, for which chromosome data are available, have  $n=13$ ,  $2n=26$  chromosomes.

Despite the divergent nature of *Acris* with respect to other hylids and the superficial similarity of *Acris* to ranids, the inescapable facts remain that *Acris* has procoelous vertebrae, an arciferal pectoral girdle, intercalary cartilages, and claw-shaped terminal phalanges—a combination of characters that seemingly inextricably ally the genus with the hylids.

### *Acris crepitans* Baird

*Acris crepitans* Baird, 1854, p. 59 [no types were designated; type locality: "Northern States generally; type locality restricted to Albany, Albany County, New York by Smith and Taylor (1950, p. 359); Albany is approximately 100 miles north of the northeasternmost known locality for the species]. Smith and Taylor, 1948, p. 77.

DIAGNOSIS: This small species, with a gray

or tan dorsum and an acutely rounded snout, is immediately distinguishable from all other Middle American hylids by the following combination of characters: tips of digits not expanded; skin on dorsum tuberculate, and that on throat and belly smooth; a black longitudinal bar, usually bordered above and below by creamy white bars, present on the posterior surface of the thigh.

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 29.0 mm., and females reach 34.0 mm. In a series of 10 males from the vicinity of Jiménez, Coahuila, México, the snout-vent length is 20.3 to 23.6 (mean, 22.5) mm.; the ratio of tibia length to snout-vent length is 0.508 to 0.609 (mean, 0.563); the ratio of foot length to snout-vent length is 0.479 to 0.578 (mean, 0.541); the ratio of head length to snout-vent length is 0.328 to 0.389 (mean, 0.355); the ratio of head width to snout-vent length is 0.322 to 0.369 (mean, 0.348), and the ratio of the diameter of the tympanum to that of the eye is 0.346 to 0.654 (mean, 0.495). Five females from the same area have snout-vent lengths of 24.6 to 25.8 (mean, 25.3) mm. and do not differ significantly from the males in proportions.

The head is narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded; in lateral profile it is round and slightly protruding beyond the margins of the lower jaw. The snout is long, and the nostrils are barely protuberant at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is barely evident, and the loreal region is inclined to be moderately thick, around the lips. A thin dermal fold extends posteriorly from the eye and angles at a point above the tympanum downward to the insertion of the arm. The fold obscures the upper and posterior edges of the tympanum, which is barely separated from the eye.

The arms are moderately short and slender; an axillary membrane is absent. Two or three small tubercles are present on the ventrolateral edge of the forearm, and a distinct transverse dermal fold is present on the wrists. The fingers are short and slender; the tips are not dilated into a disc. The subarticular tubercles are round; none is bifid. The supernumerary tubercles are absent. A large, ele-

vated palmar tubercle is present. The prepollex is barely enlarged, and in breeding males does not bear a horny nuptial excrescence. A vestige of a web is evident between the fingers (fig. 312A). The legs are long and robust; the heels of the adpressed limbs overlap by about one-third of the length of the tarsus. The tibiotarsal articulation extends to the nostril or to the tip of the snout. A distinct transverse dermal fold is present on the heel, and an elevated, flap-like tarsal fold is present. Two or three tubercles are present on the outer edge of the tarsus. The inner metatarsal tubercle is elongately ovoid and rounded. The outer metatarsal tubercle is large and conical. The toes are long and slender and do not bear expanded discs. The subarticular tubercles are moderately small and subconical; the supernumerary tubercles are either absent or minute and few in number on the proximal segments of the digits. The toes are about three-fourths webbed (fig. 312B). The webbing extends from the base of the terminal phalanx of the first toe to the base of the terminal phalanx of the second and on to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth toe and on to the base of the terminal phalanx of the fifth toe.

The anal opening is directed postroventrally near the upper level of the thighs; a short, broad anal sheath is present. Two large and several small tubercles are present below the anal opening. The skin on the dorsum is tuberculate; that on the throat, chest, and ventral surfaces of the limbs is smooth, and the skin on the posterior part of the belly is weakly granular. The tongue is narrowly cordiform, shallowly notched behind, and barely free behind. The dentigerous processes of the prevomers are small, widely separated, posteromedially inclined processes between the small, ovoid choanae. Adults of both sexes have two, three, or four teeth on each process. The vocal slits lie along the median edge of the lower jaw. The vocal sac is single, median, and subgular.

The general coloration of *Acris crepitans* is dull brown or dull gray with or without a differently colored middorsal stripe (pl. 64,

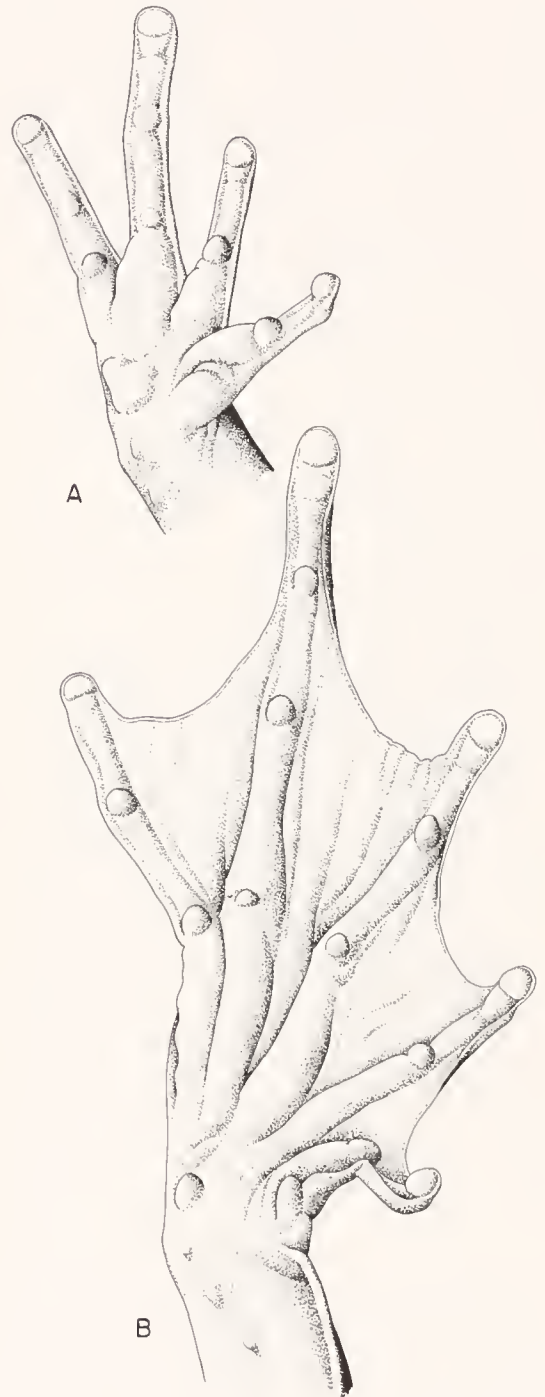


FIG. 312. Hand (A) and foot (B) of *Acris crepitans*, K.U. No. 116930.  $\times 8$ .

fig. 5). A darker brown or dull green triangular shaped mark, with the apex directed posteriorly, usually is evident on top of the head. A pair of dorsolateral darker areas usually are evident on the back, and dark brown transverse bands are present on the dorsal surfaces of the limbs. The posterior surfaces of the thighs are marked by a longitudinal black or dark brown stripe, bordered above and below by broad creamy white stripes. Distinct creamy white or pale green spots or vertical bars are present on the upper lip, and a similarly colored stripe extends from the posteroventral edge of the eye to the angle of the jaw. The anterior part of the flank is dark brown or black, whereas posteriorly, the flanks are creamy white with brown flecks. The belly is pale creamy white, or stark white and the throat is suffused or flecked with gray or brown in breeding males. Some females also have flecks on the throat. The iris is pale bronze.

I have not observed living frogs of this species from México, and consequently I am unable to determine the nature of the dorsal stripe. Pyburn (1961) noted that there were four vertebral stripe colors in *Acris crepitans* in Texas and Louisiana. He concluded that among the red, green, gray, and red-green stripes, that the green stripe is not permanent. He demonstrated that the presence of the green stripe at metamorphosis is determined by a single dominant gene and that the recessive homozygote is gray-striped. There is some evidence that green-striped frogs form a higher proportion in given populations in the eastern part of the range of the species than in the western part. Pyburn suggested that selection in relation to vegetation density might be the major cause for geographic differences in the frequency of the green stripe.

In preservative, the dorsum is dull tan to dark gray; in many individuals, markings are barely discernible. In all individuals, the dark longitudinal stripe on the posterior surfaces of the thigh is evident; however, in some specimens from México, there is no evidence of a pale stripe above the dark one.

**TADPOLES:** No tadpoles of *Acris* are known from México.

**MATING CALL:** The call of *Acris crepitans*

consists of a prolonged series of short notes, sounding like "click-click-click-click." No recordings are available from México. The analysis of a typical call from an individual in Douglas County, Kansas, reveals a note repetition rate of 128 notes per minute. The duration of the notes vary from 0.04 to 0.05 of a second, and there are approximately 70 pulses per second. The energy is spread throughout the frequency spectrum; the fundamental frequency is at about 175 cycles per second, and the dominant frequency is at about 3150 cycles per second (pl. 35, fig. 1).

**NATURAL HISTORY:** *Acris crepitans* is an aquatic-margin inhabitant. The specimens from México were obtained in riparian situations along streams in otherwise arid regions. The males usually call from shallow water or floating vegetation.

**REMARKS:** Schmidt and Owens (1944, p. 100) provided the first definite record of this species from México, based on one adult male and 10 recently transformed juveniles from La Lajita, on the Río Sabinas, near Múzquiz, Coahuila. Netting and Goin (1946, p. 253) discussed these specimens in relation to others from trans-Pecos Texas. In 1952, a field party from the University of Kansas obtained 21 specimens of *Acris crepitans* from the vicinity of Jiménez, Coahuila, México. These two localities are the only ones currently known for the species in México. Milstead (1960) included *Acris crepitans* among the 14 relict species of the Chihuahuan Desert and suggested that *Acris* had invaded the Chihuahuan Desert during pluvial times.

**ETYMOLOGY:** The specific name is Latin, meaning rattling, and apparently refers to the call of this species.

**DISTRIBUTION:** *Acris crepitans* occurs principally at low elevations from New York and northwestern Florida westward to South Dakota and eastern Colorado and New Mexico southward into Coahuila, México (fig. 310).

See Appendix 1 for the locality records of the 32 specimens examined.

#### Nomina Dubita

Two names based on specimens supposedly from Middle America cannot be assigned to known populations. In both cases holotypes are lost; thus, accurate determination



and comparisons are not possible. One other name obviously does not apply to a Middle American frog. The individual problems concerning each name are discussed below.

### *Hyla cherrei* Cope

*Hyla cherrei* Cope, 1894, p. 195 [type unknown; type locality, Alajuela, Costa Rica; R. Alfaro collector]. Günther, 1901 (1885-1902), p. 264. Taylor, 1952c, p. 846.

?*Hyla microcephala microcephala*, Duellman and Fouquette, 1968, p. 526.

The holotype (the only specimen ever referred to this name) is lost; consequently, it is necessary to rely entirely on Cope's (1894) description. On the assumption that Cope was correct when he stated "Manus almost without web; pes fully palmate" and gave the coloration as straw-colored and a narrow white stripe from the orbit to the sacrum, it is not possible with any degree of certainty to associate the name with any known population of hylid frog in Central America. The presence of a dorsolateral light stripe immediately suggests *Hyla microcephala* and *Hyla angustilincata*; the latter differs from the description of *cherrei* in other aspects of coloration, size, and webbing. Duellman and Fouquette (1968, p. 527) tentatively, and perhaps correctly, placed *cherrei* in the synonymy of *microcephala*. However, *microcephala* has the fingers about one-third webbed (more than *cherrei*) and the toes about three-fourths webbed (less than *cherrei*). Obviously, the status of the name is open to question and probably can never be settled, unless the holotype is found.

### *Hyla molitor* O. Schmidt

*Hyla molitor* O. Schmidt, 1857, p. 11 [syntype, N.M.W. No. 16494; type locality, "Chiriqui-Flusse unweit Bocca del toro," Panamá; J. von Warszewicz collector]. Brocchi, 1882, p. 40. Günther, 1901 (1885-1902), p. 279.

One faded specimen (No. 16494) in the collection of the Naturhistorisches Museum Wien purportedly is a syntype of this species. Dr. Josef Eiselt of that museum informed me (personal communication) that there is no documentation of the specimen other than a notation in Steindachner's writing that the specimen is a syntype of *Hyla molitor*. The

specimen agrees reasonably well with the detailed description given by O. Schmidt (1858, p. 245).

The snout-vent length is 36.5 mm. The fingers are slender, about one-fourth webbed, and bear small discs; the toes are about two-thirds webbed. A strong tarsal fold is present, and a heavy supratympanic fold obscures the upper part of the tympanum, which is less than one-half of the diameter of the eye. The anal region is slightly protruding, and a short anal sheath is present. There are four teeth on each of a pair of rounded elevations between the smaller round choanae. The tongue is cordiform, flattened behind, and free posteriorly for about one-fourth of its length. No vocal slits are evident; presumably the specimen is a female.

The dorsum is uniform pale brown, and the venter is creamy tan. If the specimen actually is one of the three individuals on which Schmidt based his description, the distinctive colors have faded. The coloration was described by Schmidt (1858, p. 246): "Dorsum uniformly gray, more intensive on the back, fading away laterally and on extremities; in every-day life this blue color would be called Mueller's Blau. A delicately dotted black line runs on the *canthus rostralis* from the opening of the nose to the corner of the eye. In the armpits, on the flanks and the thighs two of our three specimens have black marblings." (Free translation from the German.)

The mention of blue color laterally and black marbling on the flanks and thighs caused Duellman and Trueb (1966, p. 322) to suspect that *Hyla molitor* might be the same as the species that they named *Smilisca sila*. However, details of the description and of the supposed syntype negate that possibility. Cochran (1951, p. 58) listed, without qualification, *Hyla puma* Cope, 1885a, as a synonym of *Hyla molitor*.

Schmidt (1857, p. 12) diagnosed "*Hyla molitor*. Variet. *marmorata*. An nova species?" In 1858 (page 246) he described one individual having a snout-vent length of 38 mm. (5 mm. larger than the three specimens of *molitor* and slightly bolder dorsal coloration. *Hyla marmorata* O. Schmidt, 1857, is preoccupied by *Bufo marmoratus* Laurenti, 1768 (= *Hyla marmorata*, Daudin, 1803).

Careful examination of the supposed syn-type of *Hyla molitor* and study of Schmidt's description by Charles F. Walker, Jay M. Savage, and me have resulted in our being unable to assign the name to any known population of Central American hylids. A possibility exists that, except for the specimens obtained by Warszewicz, the species has not been discovered. A few years ago, I would have given credence to such a suggestion, but from 1964 through 1966, Charles W. Myers and I explored the lowlands and mountains of Bocas del Toro Province in Panamá without finding frogs that were referable to the species of *Hyla* named by Schmidt. Granted, this is only negative evidence, but when combined with the fact that *molitor* is unlike any *Hyla* known from Central America, we are advised to seek other possible explanations. Warszewicz obtained amphibians as a sideline to his plant collecting in Panamá and Bolivia; apparently the amphibians were not individually tagged. Consequently, the distinct possibility exists that some of the frogs reported by Schmidt as having originated in Panamá actually came from Bolivia. Unfortunately, the herpetofauna of Bolivia is so poorly known that definite association of Schmidt's supposed Panamanian species cannot be made with known populations in Bolivia at this time.

### *Hyla splendens* O. Schmidt

*Hyla splendens* O. Schmidt, 1857, p. 11 [holotype, Krakow No. 1008 (1340); type locality, "Chiriqui-Flusse unweit Bocca del toro," Panamá; J. von Warszewicz collector]. Brocchi, 1882, p. 40. Günther, 1901 (1885-1902), p. 266.

Recent discovery of the holotype has provided the opportunity to ascertain the status of this long unapplied name. The type is in rather poor condition; the color is greatly faded—no green mentioned by Schmidt (1858, p. 244) is apparent. The specimen is a male having a snout-vent length of 51.3 mm. The skin is eo-ossified with the frontoparietals, nasals, and pars facialis of the maxillaries. The skin is smooth dorsally and granular ventrally. Apparently the frog is a member of the Andean complex of *Gastrotheca*, containing the species *boliviana*, *mar-supiatum*, and *peruana*. Obviously, the frog

must have been obtained in South America by Warszewicz and subsequently mislabeled. *Hyla splendens* is not a member of the Middle American fauna. Determination of the status of the specific name *splendens* in the genus *Gastrotheca* is beyond the scope of the present paper.

### Species Inquirienda *Hyla* sp.

Stuart (1948b, p. 38) in his description of two tadpoles collected by him on February 10, 1940, in Arroyo Las Palmas at Finca Los Alpes, Departamento Alta Verapaz, Guatemala, stated: "The specimens are of particular interest owing to the tremendous development of the mouth, to form a sucking disc. Moreover, the lips are very broad and set with numerous, large papillae. These characters seem to indicate that the tadpole is specially adapted to life in swift waters, and the adults of so modified a tadpole undoubtedly live within the stream itself or in the vegetation above it."

On July 15, 1960, I obtained a single tadpole of the same species in Arroyo Las Palmas, and on August 1, 1961, I obtained a large series from the same stream. The tadpoles were found in a quiet pool in a torrential stream, where the tadpoles adhered to stones on the bottom of the pool. Attempts to raise the tadpoles to metamorphosis were unsuccessful; one individual reached developmental stage 41, at which time it had a body length of 17.8 mm. and a total length of 49.5 mm. Resorption of the tail had begun in this individual.

The largest specimens available for study are in developmental stages 35 to 37. A typical tadpole in developmental stage 35 has a body length of 17.5 mm. and a total length of 50.3 mm. The body is robust, depressed, and slightly wider than deep. In dorsal profile the snout is broadly rounded, and the posterior edge of the body is bluntly rounded. In lateral profile the snout gradually slopes anteroventrally from the nostrils, which are about one-third of the distance from the eyes to the tip of the snout. The eyes are small, widely separated, and directed dorsolaterally. The spiracle is sinistral and directed posterodorsally; the spiracular opening is below the

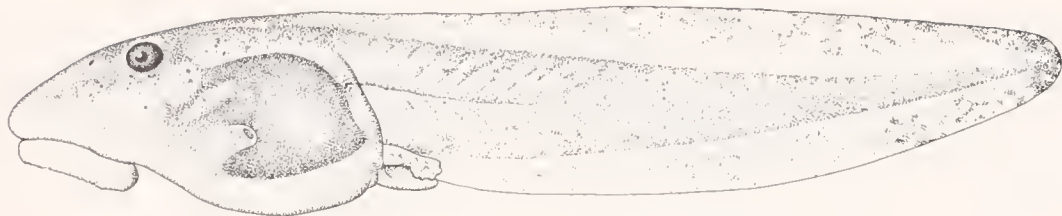


FIG. 313. Tadpole of *Hyla* sp., K.U. No. 68522.  $\times 2.5$ .

midline at a point about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is long and dextral. The tail is long and terminally rounded. The caudal musculature is robust and extends nearly to the tip of the tail. The depth of the tail is nearly constant throughout its length, and at midlength of the tail, the depth of the musculature is about equal to the depth of either fin. The dorsal fin does not extend onto the body (fig. 313).

In life, the body is dark olive-brown above. The caudal musculature has alternating dark brown and yellowish tan blotches dorsally. The iris is pale bronze. In preservative, the body is dark above and pale gray laterally and ventrally. The caudal musculature is pale tan, except dorsally where elongate dark brown blotches, narrowly separated by tan, are evident in most specimens. In small tadpoles (stage 25) the tip of the tail is noticeably darker than the rest of the tail. The dark pigment apparently disperses in larger individuals. The tadpole in developmental stage 41 has large brown spots on the sides of the body.

The mouth is very large, nearly as wide as the body, and directed ventrally. The lips are not invaginated laterally and form an entire labial disc, completely bordered by a row of small papillae. A single row of large papillae are present medially to the anterolateral part of the lip, and three or four rows of large papillae are present medially to the lower lip. The beaks are moderately robust and bear small serrations. The upper beak is broadly bell-shaped and lacks long lateral processes; the lower lip is broadly V-shaped. There are two upper and three lower rows of small teeth. All of the rows extend laterally to the lips, and all are complete (fig. 314).

Adults of three stream-breeding hylids are

known from Finca Los Alpes—*Plectrohyla guatemalensis*, *Plectrohyla quecchi*, and *Ptychohyla spinipollex*. The tadpoles of all three species are known, and none is like that described here. Tadpoles are known for all of the presently recognized species of hylids on the Atlantic slopes and highlands of Guatemala. Consequently, we are forced to conclude that the tadpoles from Finca Los Alpes belong to a species of frog not represented by adults in northern Central America.

The tadpoles from Finca Los Alpes are unique among hylid tadpoles in northern Central America and México; stream hylids in those regions either have small mouths with two upper and two lower rows of teeth or large mouths with a proliferation of tooth rows; no other tadpole from northern Central America has an enlarged mouth and only two upper and three lower rows of teeth, a common condition in hylid tadpoles in the highlands of Costa Rica and Panamá. Comparison of the tadpoles from Finca Los Alpes with those of several species from the Costa Rican high-

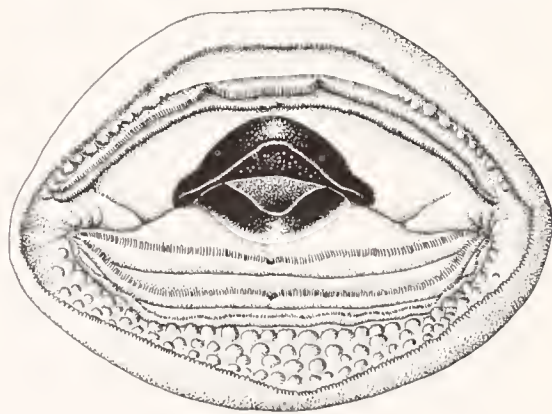


FIG. 314. Mouth of tadpole of *Hyla* sp., K.U. No. 68522.  $\times 8$ .



lands reveals that the tadpoles from Finca Los Alpes are very much like the tadpoles of *Hyla pictipes* (figs. 135 and 136). The body is broad and depressed in both, and the mouths are alike, except for two minor, but consistent, differences. In *Hyla pictipes* there are two complete rows of large papillae medially to the small fringing row anteriorly, whereas one incomplete row is present in the Guatemalan tadpoles. Furthermore, the beaks are more robust in the Guatemalan tadpoles than in *Hyla pictipes*.

The absence of other kinds of tadpoles in

northern Central America having the morphological characters of the tadpoles from Finca Los Alpes and the similarity of the tadpoles to those of *Hyla pictipes* and less so to members of the *Hyla rivularis* group, suggests that the unknown species of *Hyla* from Finca Los Alpes possibly is closely related to *Hyla pictipes*. Obviously, no conclusions can be reached until the adults are found, but because of the discontinuity of montane hylids across the Nicaraguan Depression, I am skeptical that the unknown frog in Guatemala is conspecific with *Hyla pictipes*.

## LIFE HISTORY

Despite the extensive field work on hylid frogs in Middle America and the accumulated voluminous notes, far too little is known about the life histories of most of the species. The general aspects of life history are known for about two-thirds of the species, but detailed observations are available for only ten species. Pyburn (1963, 1966) reported on *Agalychnis callidryas* and *Smilisca cyanosticta*, respectively. Zweifel (1964) and Pyburn (1967) reported on *Phrynohyas venulosa*. Breder (1946) provided excellent observations on *Hyla rosenbergi*, and Duellman (1963d) gave a detailed account of *Agalychnis annae*. Duellman and Trueb (1966) gave notes on the life histories of the species of *Smilisca* and provided detailed data on *S. phaeota*. Duellman and Klaas (1964) presented extensive notes on *Triprion petasatus*, and Trueb (1968a) included valuable life history information in her study of *Hyla lancasteri*. Detailed notes on the life histories of *Hyla miotyupanum* and *H. pseudopuma* are presented in this paper; furthermore, the tadpoles of 29 species are described for the first time. However, the tadpoles of 28 species are unknown.

Much still needs to be learned about the breeding habits and larvae of the great majority of Middle American hylids; a nearly complete absence of knowledge exists concerning reproductive cycles, growth rates, and life spans. There is a great need for some basic autecological investigations and research of reproductive cycles. These kinds of investigations, by their nature, must be carried out over long periods of time by investigators residing in Middle America.

### BREEDING

Because the males of most hylids have a voice, collectors are attracted to calling males. Consequently, information can be accumulated on the dates that males were calling either by the evidence presented in field notes or by the presence of distended vocal sacs in preserved specimens. With the full realization that males of some species may call when there is no breeding in the population, I have used the presence of calling males in order

to determine breeding times in the Middle American hylids. Presence of gravid females would be a better indicator, but females of most species are relatively scarce in collections. The accumulated data are incomplete (no data available for 23 species) and are biased by two factors. The amount of field work in Middle America has been highly seasonal; most collectors have worked there in June, July, and August. My own field work has been less limited, but it has been concentrated in the same months with only about half as much time in February, March, April, and May, somewhat less in January, a meager amount in September and December, and none in October and November. The only year-round field work carried out has been in Costa Rica and Panamá. The seasonal incidence of collectors doubtlessly is reflected in the data on breeding activity. For example, in each of the ten months of the year that I have worked in eastern México, I have found *Hyla miotyupanum* breeding; I seriously doubt if breeding activity in this species ceases in October and November, but we have no data to prove otherwise. The data are biased further by the discrepancies in the amount of information available. Our knowledge of the breeding seasons of some species is based on scores of observations, whereas data on other species are available from only one or two observations. For example, absence of records of breeding activity in *Smilisca baudinii* prior to early June on the Pacific lowlands of México is accepted as valid, because this is a common species in a well-known area. However, the two dates for breeding activity in the poorly known montane *Hyla salvadorensis* only indicate that the species does breed in June and July but do not provide any assurance that the breeding season is restricted to those months. Despite the limitations of the data, some of the results are noteworthy.

Tabulation of the number of species known to breed in any given month shows that there is an increase from 44 in April, to 50 in May, to 70 in June, and then a decrease to 63 in July and 53 in August (based on data for 91 species). The average number of breeding

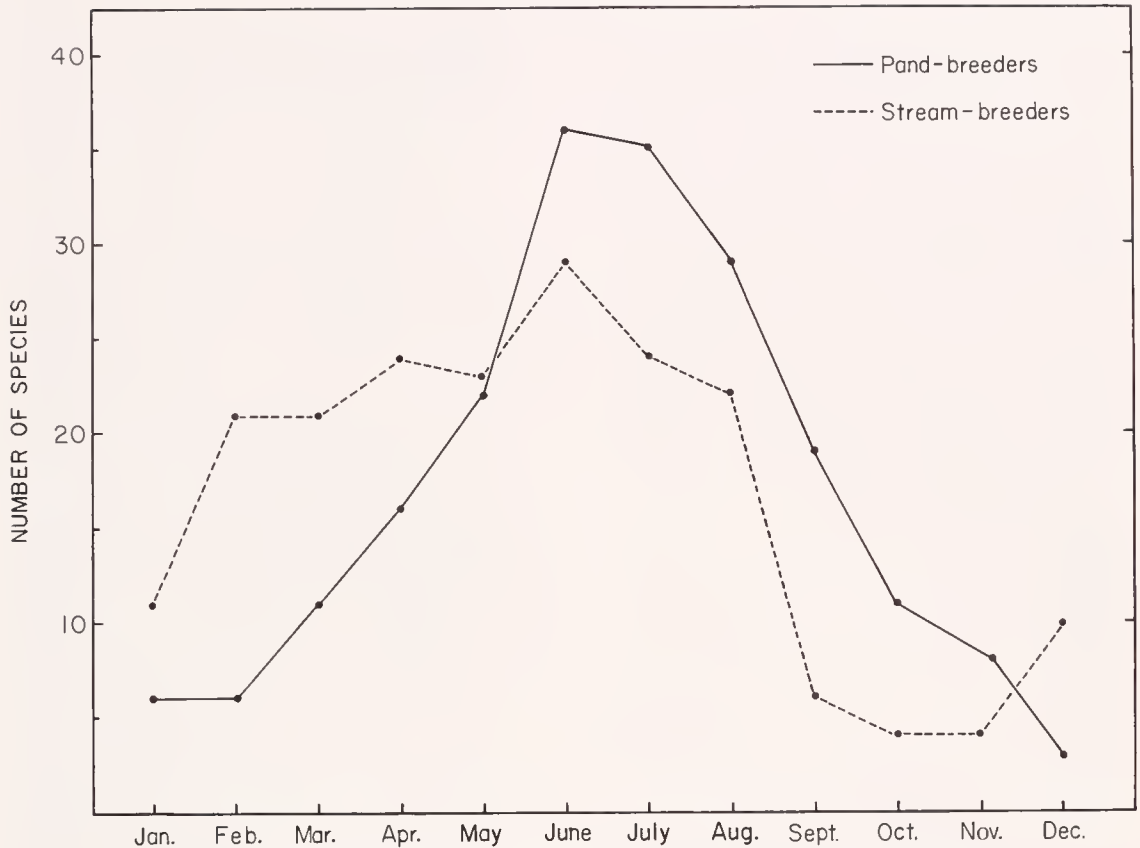


FIG. 315. Seasonal incidence of breeding activity in Middle American hylid frogs.

species in these five months is 56, whereas in the other seven months the average is 21; November with 12 breeding species is the lowest month.

Although the peak of breeding activity is in June, species with different breeding sites have different seasonal preferences (fig. 315). For example, of the 29 species known to breed in February, 21 are stream-breeders, and only six are pond-breeders. This ratio declines to 21/11 in March, 24/16 in April, and 22/23 in May. In June, July, August, September, October, and November, the pond-breeders outnumber the stream-breeders, whereas in December and January the reverse is true. Throughout much of Middle America May–November are the rainy months, and December–April are the dry months. Thus, there seems to be a close positive correlation in time of breeding in most pond-breeders with the rainy season, whereas a less noticeable

negative correlation exists with the stream-breeders.

The available data suggest that the bromeliad-breeders have extensive breeding seasons, which in *Hyla dendroscarta* and *Anotheca spinosa* extend from January through August. Breeding activity is known for four bromeliad-breeders in June. Even less information is available on those species that carry their eggs. Gravid females and females carrying eggs or young are known from May, September, and December in *Hemiphractus panamensis*. Calling males of *Gastrotheca ceratophrys* have been heard in March through July, and those of *Gastrotheca nicefori* have been heard in January.

The seasonal activity in many stream-breeding species is understandable when one realizes that most of these species inhabit humid montane forests that are moist throughout the year. Secondly, and perhaps more



significantly, the streams are usually clear and more quiet in the drier seasons. At the height of the rainy season streams in many places become rushing torrents of murky water that roll boulders along the stream beds; such streams are poor habitats for fragile tadpoles. For example, *Hyla miotympanum* calls throughout the dry season along a quiet stream, 3 kilometers southwest of Huatuseo, Veracruz, México; tadpoles of this species are abundant in the stream. In June and July the stream, swollen by heavy rains, roars through the ravine. Few, if any, adults of *Hyla miotympanum* are found on vegetation along the stream. It is doubtful if tadpoles can survive in the stream.

The positive correlation of breeding activity with the rainy season in many pond-breeders is understandable, because so many of these species utilize temporary ponds that are formed by the heavy rains. Furthermore, many lowland areas are suitable for amphibian activity only during the rainy season. In the dry season the frogs are secreted in bromeliads, elephant-ear plants under sheaths of banana plants, or in other moisture-holding hiding places unknown to collectors.

Little conclusive information is available on the duration of the breeding season. On the bases of apparent year-round activity and the presence of tadpoles in many stages of development at widely scattered times during the year, it is reasonable to assume that many of the montane stream-breeders, such as *Plectrohyla*, *Ptychohyla*, and the *Hyla rivularis*, and *uranochroa* groups, have extended breeding seasons. Several of the species apparently breed throughout the year. On the other hand, prolonged breeding seasons are unusual in lowland pond-breeding species and seemingly exist only in a few species living in rain forest.

Thus far, the discussion of breeding has been concerned with entire species. Further insights into some of the situations, and some new problems are apparent when populations of one species are examined. Unfortunately, only incomplete data, at best, are available. Although it is highly probable that the wide ranging montane species *Hyla miotympanum* breeds throughout the year, I have just mentioned that at one locality breeding activity

ceases at the height of the rainy season. Populations of this species at high elevations in Hidalgo were inactive in January and February, whereas populations at lower elevations were breeding. In the Caribbean lowlands, receiving abundant rain throughout the year, in lower Central America *Hyla chraaccata* apparently breeds year-round, but to the north, in southern México, where a definite dry season occurs, the species breeds only in the rainy season. These are only two examples of species having wide altitudinal or latitudinal distributions and exhibiting altitudinal or geographic variation in breeding seasons.

The available records for *Triprrion spatulatus* and *Phrynohyas venulosa* indicate that these species have breeding seasons from June through August and April through August, respectively. However, these are the accumulated records of many years from throughout the range of the species. Both species, especially *Triprrion*, emerge for breeding only after torrential rains. Experience has shown that the frogs emerge and breed on the night following a heavy rain and then disappear again, in many instances not to reappear until the next year. Consequently, where the data indicate a breeding season of three months for the species, the breeding activity in a given population may be limited to a period of a few hours in any given year.

Another nearly unknown aspect of the breeding biology of hylid populations concerns the reproductive cycles of individuals in the population. In many places it is possible to hear frogs of a particular species calling every night for many consecutive weeks or even months, but are the same individuals calling throughout that period of time? Also, we can ask but cannot answer: does one individual breed more than once a year? Some hints to the answers are provided by data on *Hyla pseudopuma* and *Agalychnis callidryas*. At Tapantí, Costa Rica, *Hyla pseudopuma* was breeding from early April until mid-May, when breeding activity ceased until August. These data suggest that there are at least two breeding seasons in this population, but we do not know if the same individuals breed in both seasons. Some gravid females of *Agalychnis callidryas* taken early in the breeding season contained ovulated eggs plus

another complement of ovarian eggs. Most individuals taken later in the season contained only one complement. These meager data suggest that individual females of *Agalychnis callidryas* breed twice in a given breeding season.

### EGGS

Eggs are known of only 45 species of hylid frogs living in Middle America. The following discussion is based on my own observations and the scant information available in the literature.

The majority of Middle American hylids deposit their eggs in water. Of those groups for which eggs and/or tadpoles are known, we can be reasonably sure that 35 species deposit their eggs in ponds and 52 species lay their eggs in streams. The following species are known to deposit their eggs in masses, either free or attached to vegetation, in ponds: *Acris crepitans*, *Pseudacris clarkii*, *Pternohyla fodiens*, *Triprion petasatus*, and the following species of *Hyla*—*boans*, *boulengeri*, *elaeochroa*, *euphorbiacea*, *eximia*, *loquax*, *microcephala*, *phlebotodes*, *plicata*, *pseudopuma*, *regilla*, *rosenbergi*, *staufferi*, and *walkeri*. Two of the latter species (*boans* and *rosenbergi*) deposit their eggs in shallow basins constructed by the males in mud or gravel at the edges of rivers or sluggish streams. Thus, although the oviposition sites are adjacent to flowing water, the eggs are actually deposited in still water.

Five species are known to spread their eggs in a film on the surface of the water in ponds; these are *Hyla rufitela*, *Phrynohyas venulosa*, *Smilisca baudinii*, *Smilisca eyanosticta*, and *Smilisca phacota*.

Of the 52 Middle American hylids that are known, or suspected, to deposit their eggs in streams, eggs of only five species are known. *Hyla arenicolor* deposits small clumps of eggs in quiet pools, and *Hyla cadaverina* deposits single eggs in the same situations. Eggs of *Hyla colymba* were found under a rock in a stream (Dunn, 1924), and those of *Hyla sumichrasti* were found attached to a dead leaf between stones in a stream (Starratt, 1960a). The eggs of *Hyla miotympanum* are attached to the lee sides of rocks or to vegetation in streams. Empty egg cases at-

tached to rocks in streams known to be inhabited only by *Plectrohyla* are a good indication that at least some of the species in that genus deposit their eggs on rocks in streams. I suspect that eggs are deposited in streams by all of the species of *Plectrohyla* and *Ptychohyla* and by the members of the following species groups of *Hyla*: *bistincta*, *erythroma*, *miotympanum*, *mixomaculata*, *pictipes*, *pinorum*, *ritularis*, *salvadorensis*, *sumichrasti*, *taeniopus*, and *uranochroa* groups.

Some hylids deposit their eggs on vegetation above water. Presumably all of the Middle American species of *Agalychnis* and *Phyllomedusa* (eggs not known for *A. litodryas* and *P. venusta*), and *Pachymedusa dactinicolor* attach clumps of eggs on leaves or branches of bushes or trees overhanging ponds. *Hyla ebraccata* and at least some of its relatives comprising the South American *Hyla leucophyllata* group usually deposit their eggs in a single layer on leaves of emergent herbs in ponds. Two species of *Hyla* (*lancasteri* and *thorectes*) are known to lay their eggs on vegetation overhanging mountain streams.

Four species are known to deposit their eggs in water above the ground. Eggs of *Anotheca spinosa* have been found in water-filled cavities in trees and in bromeliads; *Hyla bromeliacia*, *dendrocarta*, *zeteki*, and probably *picadoi* lay their eggs in bromeliads. It is highly likely that at least some of the fringe-limbed tree frogs of the *Hyla miliaria* group utilize tree holes for egg deposition.

In *Hemiphractus panamensis*, eggs are carried in depressions on the back of the female; there the eggs develop directly into small frogs. The eggs are carried in a dorsal brood pouch in *Gastrotheca ceratophrys*; presumably these eggs also undergo direct development. The same condition exists in *Gastrotheca nicefori*.

The numbers of eggs produced by individual females of various species seems to vary directly with differences in size of the species. This correlation holds true in groups of related species having the same kinds of life history, such as the *Smilisca baudinii* group (Duellman and Trueb, 1966). Stream-breeding species tend to have far fewer eggs than do pond breeders. Examples of the lat-

ter category include: *Smilisca baudinii* (2620-3320, mean 2960 eggs), *Smilisca cyanosticta* (910), *Smilisca phaeota* (1665-2010, mean, 1848), and *Tripurion petasatus* (1750). A variety of stream-breeders have fewer, but larger eggs: *Hyla miotympanum* (120), *Hyla pictipes* (126), *Hyla sumichrasti* (50), *Hyla uranochroa* (69), *Ptychohyla euthysanota* (155), and *Ptychohyla schmidtorum* (191). Specialized methods of egg deposition seem to be correlated with a decrease in the number of eggs. The species of *Agalychnis* all of which suspend their eggs on vegetation over ponds, have fewer eggs than do those species that deposit their eggs in ponds; for example, *Agalychnis annae* has 47 to 162 (mean, 102) eggs, and *Agalychnis callidryas* has 39 to 108 (mean, 78) eggs. The two species that deposit their eggs on vegetation over streams produce very few, large eggs. Three clutches from *Hyla thorectes* contained 10 eggs each, and two clutches from *Hyla lancasteri* contained 20 to 23 eggs. The same reduction apparently holds for bromeliad breeders; one seemingly complete clutch from *Hyla bromeliacia* contained 14 eggs and a gravid female of *Hyla zeteki* contained 24 eggs. Parental care by means of carrying eggs and young also results in fewer and larger eggs. One female of *Gastrotheca ceratophrys* contained nine eggs in the brood pouch. Numbers of ovarian eggs, egg scars on dorsum, or attached young in *Hemiphractus panamensis* vary from 12 to 14.

Primitive hylids probably deposited their eggs in clumps in ponds. From this original type the other modes of deposition probably were evolved independently. Each of the secondary oviposition habits possibly evolved several times. The two groups of frogs in Middle America that deposit their eggs on vegetation over ponds (phyllomedusines and *Hyla leucophyllata* group) are distantly related and certainly evolved their oviposition habits independently. The same certainly is true for the surface-film deposition habit and for the bromeliad deposition habits of *Anotheca* and the species of *Hyla* (probably independently in two groups of *Hyla*). The stream habit apparently evolved twice in Middle American hylids, and independently a

third time in the South American *Hyla colymba* group.

### TADPOLES

The morphological adaptations of tadpoles have been discussed in detail in a preceding section (Taxonomic Characters and Criteria in Hyliid Frogs). Only a brief summary of the ecology of tadpoles is presented here. Tadpoles are known for 83 species of Middle American frogs. These include all of the genera that have an aquatic larval stage and all of the species groups of *Hyla*, except the *Hyla miliaria* group. The following have tadpoles that develop in ponds: *Pachymedusa*, *Agalychnis*, *Phyllomedusa* (part), *Phrynohyas*, *Smilisca* (part), *Pterohyla*, *Tripurion*, *Acris*, *Pseudacris*, and the following groups of *Hyla*—*albomarginata*, *boans*, *eximia* (part), *godmani*, *leucophyllata*, *microcephala*, *parviceps*, *picta*, *pseudopuma*, *rubra*, and *versicolor* (part) groups. Stream-adapted tadpoles occur in *Phyllomedusa* (some South American species), *Smilisca* (part), *Pterohyla*, *Ptychohyla*, and the following groups of *Hyla*: *bipectinata*, *colymba*, *eximia* (*cadaverina*), *hazellae*, *lancasteri*, *miotympanum*, *mixomaculata*, *pictipes*, *pinorum*, *rivularis*, *salvadorensis*, *sumichrasti*, *taeniopus*, *uranochroa*, and *versicolor* (*arenicolor*) groups. The tadpoles of *Anotheca* and the *Hyla bromeliacia* and *zeteki* groups develop in bromeliads.

Among the kinds of tadpoles that develop in ponds, there are some pelagic types, principally belonging to the phyllomedusine genera. Other pond tadpoles, especially those of species in the *Hyla rubra*, *leucophyllata*, and *microcephala* groups, inhabit parts of ponds choked with vegetation. No highly adapted surface-feeding tadpoles are known among the Middle American hylids.

Stream tadpoles exhibit various degrees of modification in depression of body, elongation of tail, reduction of caudal fins, and enlargement of the mouth. In most stream tadpoles the mouth is used to adhere to stones in the stream. The trend in modification for this behavior is correlated with a morphological progression from a small anteroventral mouth with an incomplete border of labial papillae to a greatly enlarged ventral



mouth with a complete border of labial papillae. In the stream tadpoles in the Mexican and Guatemalan highlands the enlargement of the mouth is accompanied by an increase in the number of tooth rows from the basic pattern of 2/3 to as many as 7/11. Although some of the stream tadpoles in the highlands of lower Central America have mouths equally as large as those in the former group, none has more than 2/3 tooth rows, except *Hyla legleri* and *Hyla colymba*, both of which belong to groups that evolved elsewhere. In two groups of montane hylids (*Hyla uranochroa* and *Ptychohyla schmidtorum* groups) the tadpoles exhibit a different kind of buccal modification for life in streams. The mouth is funnel-shaped with short rows of teeth and few papillae. In general, the various kinds or stages of modifications seem to be poorly correlated with microhabitats in the mountain streams. However, in some streams, where a variety of adaptive types of tadpoles live, some ecological segregation is evident. Tadpoles having relatively small mouths and few rows of teeth are more commonly found in quieter parts of the stream, whereas those having very large mouths most frequently are found in riffles or adhering to stones in fast water. The tadpoles with funnel mouths usually adhere to detritus in pools in the stream.

The bromeliad tadpoles of the *Hyla bromeliae* group have greatly elongated tails with low fins, depressed bodies, and small mouths with 2/4 tooth rows. The egg-eating arboreal tadpoles of *Hyla zeteki* and *Anotheca spinosa* have more robust bodies, proportionately shorter tails, and moderate-sized mouths with a reduced number of tooth rows (mouth anteroventral with 2/2 rows in *Anotheca* and anterodorsal with 1/1 rows in *Hyla zeteki*.)

The tadpoles of all frogs are forced to adapt to environments imposed upon them by the egg deposition sites selected by the adults. Selective pressures obviously have been important in molding the variety of morphological conditions and behavioral patterns exhibited by the hylid tadpoles. In cases of sympatry the various kinds of modifications

that seem to be correlated with ecological segregation possibly are the result of natural selection due to pressures of interspecific competition among the tadpoles of various species.

#### DURATION OF DEVELOPMENT

Very little is known about the duration of larval development in Middle American hylids. Duellman (1963d) noted that tadpoles of *Agalychnis annae* required 247 days from hatching to metamorphosis; in light of the 79 days reported for *Agalychnis callidryas* (Pyburn 1963) and the 79 to 81 days necessary for *Hyla pseudopuma* from the same pond as the tadpoles of *Agalychnis annae*, it is likely that the development of the latter was unduly prolonged by suboptimal laboratory conditions. The duration of larval development has been reported as 37 and 47 days in *Phrynohyas venulosa* by Zweifel (1964) and Pyburn (1967), respectively, and 40 days in *Smilisca cyanosticta* by Pyburn (1966).

The relatively rapid development of lowland species (*Phrynohyas venulosa* and *Smilisca cyanosticta*) as compared with the longer period of development in the montane *Hyla pseudopuma* possibly is correlated with the temperature of the water in which the tadpoles develop. However, the rapid rate of development in many of the lowland species that utilize temporary ponds might be an adaptation to the temporary nature of their habitat.

Although data are lacking on the duration of larval development in stream tadpoles, I have kept tadpoles of many stream-breeding species. My general impression is that the rate of development in these stream tadpoles is much slower than in pond breeders. Stuart (1951) suggested that the tadpoles of *Plectrohyla guatemalensis*, which develop in very cold water, may require more than one year to complete their development. The same may be true for other high montane species, such as *Hyla robertsoni* and *Hyla charadriicola*.

## PHYLOGENY AND ZOOGEOGRAPHY

### RELATIONSHIPS OF THE SPECIES

A determination of the phylogenetic relationships of all of the Middle American hyliid frogs is not possible until the taxonomy of the South American species is much better known. Conclusions concerning the interspecific relationships of species can be reached by phenetic methods alone, based solely on the objective comparison of character states. These results provide a measure of similarity of the taxa but do not account for the many apparent cases of convergence. Some proponents of the phenetic approach argue that when a sufficiently large number of characters are used the problem of convergence is eliminated. An analysis of 83 characters in Middle American hyliids is inconclusive in some respects, because not all characters were available for all species. Tadpoles of several species are unknown, and skeletal material is not available for some species. Separate analyses of these three groups of characters resulted in many similarities of arrangement but also some major discrepancies, especially in the case of larval characters.

A phylogenetic approach is hampered by the subjective designation of primitive and derived states of characters. Again the problem of convergent and parallel evolution complicates this method of analysis. The problems of a strictly numerical analysis of the Middle American hyliids have yet to be solved to my satisfaction. Consequently, I have undertaken a less sophisticated approach based primarily on those characters for which primitive and derived states can be determined with some reasonable degree of assurance. Through trial and error various natural phyletic and geographic groupings were assembled. These were then subjected to analysis and comparison; thus the problem of convergence was minimized by a prior elimination of groups having characters in common but apparently having entirely different geographic and phyletic histories. For example, the presence of a prepollical spine in males in the *Hyla boans* group and in *Plectrohyla* does not relate these two groups, the latter of which is endemic to the highlands of Nuclear Central America, whereas the former

is an Amazonian group that barely enters Middle America.

The 52 principal morphological characters used in determining the relationships of the species are listed below. The assumed primitive character state is given a value of 0, and successively derived (advanced) states are evaluated 1, 2, 3, and so on. In those characters in which the evolution of a character has diverged in two directions, the secondary derivatives are evaluated -1, -2, and so on. Most of these characters are discussed in detail in the section of taxonomic characters and criteria in hyliid frogs. Tilien (1965) presented a summary of evolutionary trends in frogs, but Trueb (1970a) took exception to his remarks on dermal roofing bones on the skull.

#### A. Nature of head:

- 0. Normal
- 1. Modified (co-ossified and/or with bony projections).

#### B. Shape of snout (lateral profile):

- 1. Truncate
- 0. Round
- 1. Acuminate
- 2. Protruding

#### C. Rostrum:

- 1. Vertical keel
- 0. Normal
- 1. Fleshy proboscis

#### D. Tympanum:

- 0. Present, well-defined
- 1. Present but reduced in size
- 2. Concealed

#### E. Mental gland:

- 0. Absent
- 1. Present

#### F. Palpebral membrane:

- 0. Clear
- 1. Reticulated

#### G. Vocal sac:

- 1. Absent
- 0. Single, median, subgular
- 1. Single, bilobed
- 2. Paired, subgular
- 3. Paired, lateral

#### H. Dorsal skin:

- 0. Smooth
- 1. Tuberculate

#### I. Osteoderms:

- 0. Absent
- 1. Present

#### J. Ventrolateral glands:

- 0. Absent
- 1. Present

- K. Axillary membrane:
  - 0. Absent
  - 1. Present
- L. Thumb:
  - 0. Shorter than 2nd finger
  - 1. Longer than 2nd finger
- M. Prepollex:
  - 0. Normal
  - 1. Enlarged
  - 2. Projecting spine
- N. Nuptial excrescence:
  - 1. Absent
  - 0. Present
  - 1. Modified (such as cluster of spines)
- O. Metatarsal tubercle:
  - 0. Normal
  - 1. Modified (such as spatulate)
- P. Calcar:
  - 0. Absent
  - 1. Present
- Q. Dermal fringes on limbs:
  - 0. Absent
  - 1. Present
- R. Anal Opening:
  - 0. Posterior
  - 1. Posteroventral
  - 2. Ventral
- S. Brood pouch:
  - 0. Absent
  - 1. Present
- T. Premaxillary (inclination of alary process):
  - 1. Anteriorly
  - 0. Vertical
  - 1. Posteriorly
- U. Premaxillary (shape of alary process):
  - 0. Single
  - 1. Bifurcate
- V. Maxillary (pars facialis):
  - 2. Absent
  - 1. No articulation with nasal
  - 0. Partial articulation with nasal
  - 1. Complete articulation with nasal
- W. Maxillary (posterior process of pars facialis):
  - 0. Articulation with maxillary process of nasal
  - 1. No articulation with maxillary process of nasal
  - 2. Absent
- X. Prevomer (dentition):
  - 0. Dentate
  - 1. Edentate
  - 2. Odontoids
- Y. Palatine:
  - 0. Present, articulating with sphenethmoid and maxillary
  - 1. Present, articulating with maxillary or sphenethmoid, but not both
  - 2. Present, articulating with neither sphenethmoid nor maxillary
  - 3. Absent
- AA. Palatine (ventral surface):
  - 0. Smooth
  - 1. Smooth ridge
  - 2. Irregular ridge
  - 3. Serrate ridge
  - 4. Serrate ridge and odontoids
- BB. Nasal
  - 1. Reduced
  - 0. Normal
  - 1. Expanded
- CC. Dermal sphenethmoid:
  - 0. Absent
  - 1. Present
- DD. Frontoparietal fontanelle:
  - 0. Open
  - 1. Covered
- EE. Prootic:
  - 0. Crista parotica articulating with squamosal
  - 1. Crista parotica not articulating with squamosal
- FF. Parasphenoid:
  - 0. Edentate
  - 1. Odontoids present
- GG. Pterygoid:
  - 0. Medial ramus articulating with prootic
  - 1. Medial ramus not articulating with prootic
- HH. Pterygoid (position of articulation of anterior ramus with maxillary):
  - 0. Posterior
  - 1. Anterior
- II. Squamosal:
  - 0. Anterior arm not extending to maxillary
  - 1. Anterior arm extending to maxillary
- JJ. Quadratojugal:
  - 0. Present, articulating with maxillary
  - 1. Present posteriorly
  - 2. Absent
- KK. Dermal roofing bones:
  - 0. Normal
  - 1. Expanded
- LL. Vomerine tooth patches:
  - 1. Reduced or absent
  - 0. Normal
  - 1. Enlarged and modified
- MM. Prenasal:
  - 0. Absent
  - 1. Present
- NN. Internasal:
  - 0. Absent
  - 1. Present
- OO. Mandibular Odontoids:
  - 0. Absent
  - 1. Present
- PP. Development:
  - 0. Aquatic larvae
  - 1. Direct development
- QQ. Tadpole Body Shape:
  - 1. Deep



- 0. Robust
  - 1. Ovoid
  - 2. Depressed
- RR. Spiracle (position):
  - 0. Lateral
  - 1. Ventrolateral
  - 2. Ventral
- SS. Caudal musculature:
  - 1. Niphicercal
  - 0. Normal
  - 1. Massive
- TT. Caudal Fins:
  - 1. Reduced
  - 0. Equal
  - 1. Deep
- UU. Dorsal Fin:
  - 1. Reduced
  - 0. Normal
  - 1. Extending anteriorly onto body
- VV. Mouth (position):
  - 1. Ventral
  - 0. Anteroventral
  - 1. Terminal
  - 2. Dorsal
- WW. Mouth (size):
  - 1. Funnel
  - 0. Normal
  - 1. Large
  - 2. Immense
- XX. Labial papillae:
  - 1. Absent
  - 0. Incomplete
  - 1. Complete
- YY. Beaks:
  - 0. Normal
  - 1. Modified
- ZZ. Tooth rows:
  - 3. 0/0
  - 2. 1/1
  - 1. 2/2
  - 0. 2/3
  - 1. 2/4 or 2/5
  - 2. 3/3, 3/4, 3/5, or 3/6
  - 3. 4/6
  - 4. 6/9
  - 5. 7/10 or 7/11

A measure of divergence was calculated by separating each character into its number of states (for example, two states of the nature of the dorsal skin and five states of condition of the vocal sac). Consequently, 143 character states were used. The presence or absence of a state was noted for each species; the number of differences in character states in comparison with other species was noted for each species. The number of differences was divided by the total number of character states used in order to arrive at a measure of divergence. The absolute number of dif-

ferences was not used, because the number of character states was not constant for all species; for example, a comparison of species, one of which lacked data on tadpoles, was based on 105 character states, instead of 143.

The resulting measurement (or index) of divergence tends to group similar species and to separate dissimilar species. If two species share all character states their divergence index is 0; if they differ in all character states their divergence index is 1. An example is illustrated in a divergence matrix of the Middle American species of *Agalychnis*, *Acris*, and *Anotheca* (table 60). In this example the mean divergence index for the seven species of *Agalychnis* is 0.053 whereas the divergence index of *Acris* and *Anotheca* from all *Agalychnis* is 0.156 and 0.184, respectively. A highly divergent species, *Triprrion pectatus*, differs from *Agalychnis callidryas* by an index of 0.287.

This kind of phenetic analysis is useful but can lead to an understanding of phylogeny only when utilized with information concerning the evolutionary trends in characters. By tallying the number of primitive characters, first stage derived characters, and so on, in any given species, it is possible to determine the species having the greatest number of derived characters. Comparison of the derived characters leads first to the elimination of those characters that are common to all of the species in a given group and secondly to an understanding of the divergence in the derived characters. For example, among the external characters in *Agalychnis*, three species differ from all others by possessing one unique character. Examination of which characters are involved reveals that *calcarifer* is unique by having a calcar, whereas *lito-dryas* and *spurrelli* are alike, but different from *calcarifer* by having an expanded prepollex.

The above described method of analysis was used on the members of the Middle American hylid fauna that are considered to have arisen in Middle America and to form the Mesoamerican fauna (figs. 316-318). An analysis of the South American and North American groups in Middle America would be pointless without considering their multitudinous, and as yet unstudied, relatives.

TABLE 60

Sample Divergence Matrix for Nine Species. The numbers on the right side are the absolute number of differences in character states; the numbers on the left side are the calculated degree of difference.

See text for explanation.

	<i>Agalychnis annae</i>	<i>Agalychnis calcarifer</i>	<i>Agalychnis callidryas</i>	<i>Agalychnis litodryas</i>	<i>Agalychnis moreletii</i>	<i>Agalychnis saltator</i>	<i>Agalychnis spurrelli</i>	<i>Acris crepitans</i>	<i>Anotheca spinosa</i>
<i>Agalychnis annae</i> .....	X	6	4	2	2	4	4	20	28
<i>Agalychnis calcarifer</i> .....	0.13	X	4	6	6	4	6	8	10
<i>Agalychnis callidryas</i> .....	0.03	0.08	X	2	4	2	4	20	26
<i>Agalychnis litodryas</i> .....	0.04	0.13	0.04	X	2	4	2	10	10
<i>Agalychnis moreletii</i> .....	0.01	0.13	0.03	0.04	X	4	2	20	28
<i>Agalychnis saltator</i> .....	0.03	0.08	0.01	0.08	0.03	X	2	20	24
<i>Agalychnis spurrelli</i> .....	0.03	0.13	0.03	0.04	0.01	0.01	X	22	26
<i>Acris crepitans</i> .....	0.14	0.17	0.14	0.17	0.14	0.14	0.15	X	22
<i>Anotheca spinosa</i> .....	0.20	0.21	0.18	0.17	0.18	0.17	0.18	0.15	X
Character States .....	143	48	143	48	143	143	143	143	143

ZOOGEOGRAPHY OF MIDDLE AMERICAN HYLID FROGS

Complex physiography and climatic patterns, diversity of environments, and histories of land masses and associated faunas combine to give Middle America a highly diversified fauna composed of many species. The region includes desert, tropical rainforest, and high montane forests. Elevations range from sea level to 5600 meters. In order to gain an understanding of the zoogeography of the Middle American hylid frogs it is necessary to examine the various environmental factors affecting their distributions, the distribution of environmental types in the region, the effect of altitude in correlation with the two previous sets of data, and lastly the geographic patterns of the frogs.

ECOLOGICAL DISTRIBUTION

On the basis of field observations it is possible to determine such aspects of the ecology as general habitat, microhabitat, calling site, oviposition site, tadpole habitat, and seasonal and diel activity. However, very few quantitative measurements are available.

Moisture requirements are unknown for Middle American hylids. Stebbins and Hendrickson (1959) and Brattstrom (1963) presented some data on body temperatures of a few Middle American hylids—*Acris crepitans*, *Hyla cadaverina*, *H. crepitans*, *H. dendroscarta*, *H. picta*, *H. regilla*, *H. staufferi*, and *Smilisca baudinii*. Brattstrom (1968) studied thermal acclimation with respect to altitude and latitude in several frogs, including the following Middle American species: *Acris crepitans*, *Hyla cadaverina*, *H. regilla*, *H. smithii*, *H. staufferi*, *H. walkeri*, *Pachymedusa dacnicolor*, *Pternohyla fodiens*, *Smilisca baudinii* and *S. phaeota*. The data presented in these papers are extremely meager and have very limited application to an understanding of the thermal requirements of the Middle American hylids under natural conditions. Brattstrom (1968, p. 110) concluded that: "Tropical anurans do not have a narrow range of acclimation, or capacity for physiological adjustment. Instead the entire thermal régime of the more southern species is higher than for northern forms. . . . High altitude forms of the United States and México act similarly, in terms of their ability to acclim-

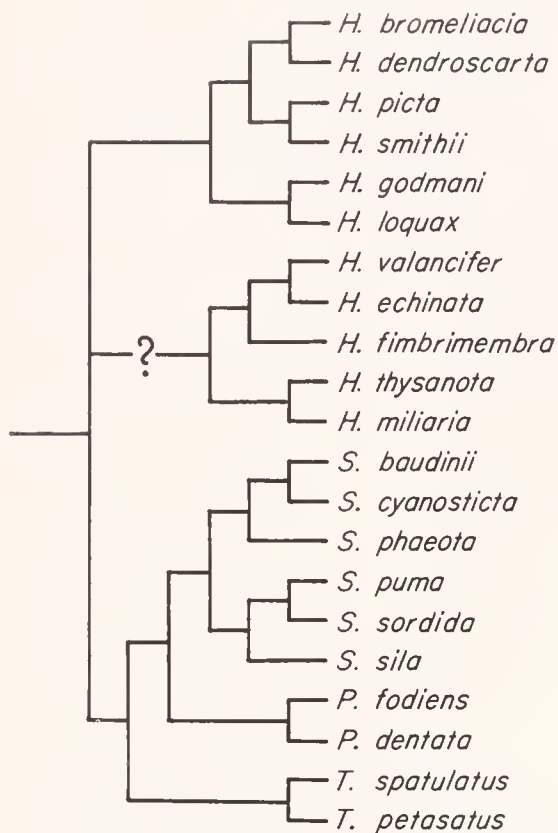


FIG. 316. Phenogram of the Lowland Component of the Mesoamerican hylids. *H.*=*Hyla*, *P.*=*Ptenohyla*, *S.*=*Smilisca*, *T.*=*Triprion*.

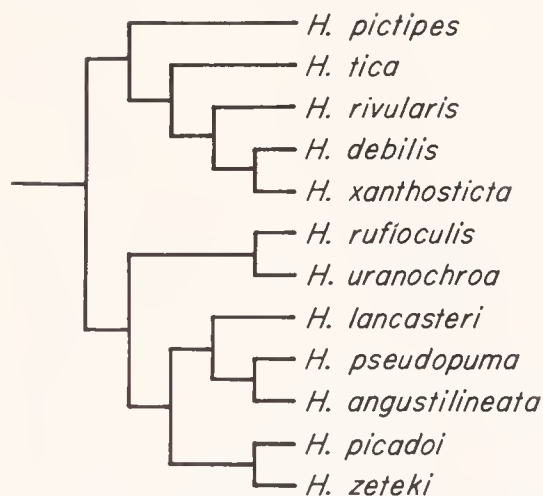


FIG. 317. Phenogram of the Lower Central American Highland Component of Mesoamerican hylids. *H.*=*Hyla*.

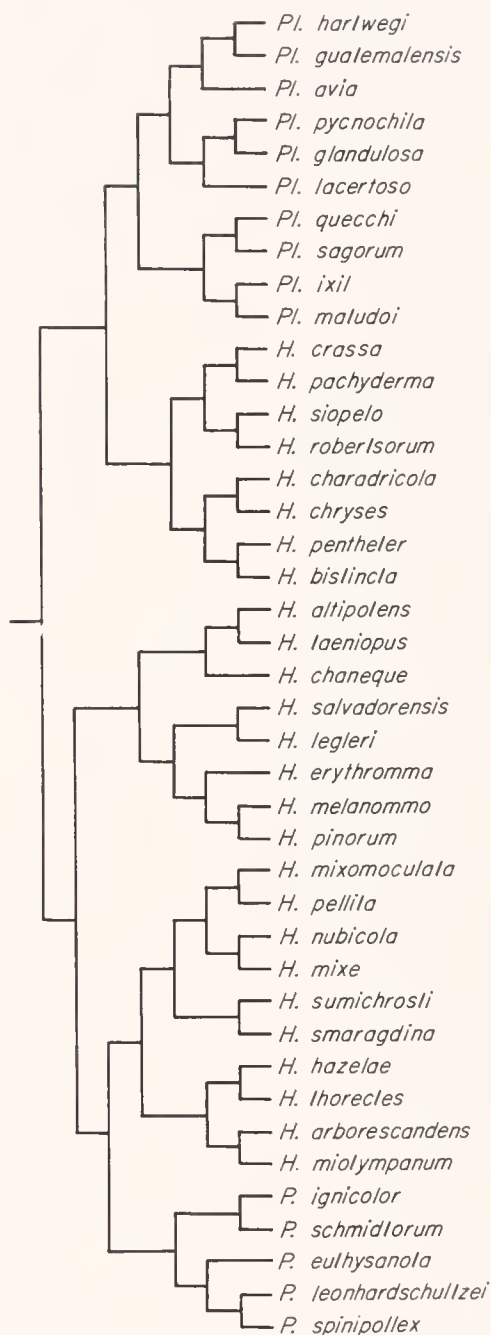


FIG. 318. Phenogram of the Nuclear Central American and Mexican Component of Mesoamerican hylids. *H.*=*Hyla*, *P.*=*Ptychohyla*, *Pl.*=*Plectrohyla*.



ate, to temperate forms of equivalent thermal latitudes."

Brattstrom and Warren (1955) and Fitch (1956) presented data which show that temperature influences activity in such temperate hylids as *Acris crepitans*, *Hyla regilla*, *H. versicolor*, and *Pseudacris triseriata*. Zweifel (1955) and Storm (1960) noted the correlation between body temperature and activity in the heliothermic montane *Rana muscosa* and *Rana aurora*, respectively.

Of the strictly major physical environmental factors, I believe that moisture is far more important than temperature in the ecological and geographic distribution of Middle American hylid frogs. However, the distribution of moisture throughout the year, either in the form of rainfall or mist is also important. A subtle, yet significant relationship exists between temperature and rainfall. These two climatic variables determine the amount of moisture retained in the environment. This environmental characteristic is roughly comparable with the evapotranspiration rate as correlated with biotemperature by Holdridge (1964).

The relationship between temperature and precipitation and the distribution of hylid frogs can be demonstrated by comparing temperature and rainfall with hylid distributions in the lowlands of the Isthmus of Tehuantepec. Climatic data are for Minatitlán on the Atlantic lowlands and Salina Cruz on the Pacific lowlands and are taken from Contreras Arias (1942). The monthly mean temperatures vary from 23.2 to 28.9°C. (mean, 26.2°C.) at Minatitlán and from 24.8 to 28.3°C. (mean, 26.6°C.) at Salina Cruz. At Minatitlán the mean annual precipitation is 3085 mm. with April being the driest month with 36 mm. and September the wettest with 642 mm. At Salina Cruz the mean annual rainfall is 1040 mm. with March devoid of rain and June the wettest month with 334 mm. Ten species of hylids inhabit the lowlands of the Isthmus of Tehuantepec. Six species occur only on the Atlantic lowlands; two species are found only on the Pacific lowlands, and only two species occur on the lowlands on both sides of the isthmus, although there are no physical barriers to their dispersal.

With respect to mean annual temperature

and total amount of rainfall, Liberia in the arid tropical forest of Guanacaste, Costa Rica, is not much different from Turrialba in the upper humid tropical forest on the Caribbean slopes of Costa Rica. At Liberia the mean temperature in 1964 was 22.9°C. with a range of monthly means from 21.4°C. to 26.0°C., at Turrialba the mean was 22.1°C. (range, 20.6° to 23.0°C.). (Anonymous, 1965). In 1964 Liberia had 1739 mm. of rain, and Turrialba had 1926 mm. Although there is little difference in the temperature and the total amount of rainfall, there is considerable difference in the distribution of the rainfall at the two sites; at Turrialba rain fell on 217 days and at Liberia only on 114 days, with no rain in January-March. The difference in seasonal distribution of rainfall is evident in the deciduous nature of the vegetation at Liberia as contrasted with the luxuriant evergreen vegetation at Turrialba. Nine species of hylids are known from Turrialba, whereas only four occur at Liberia; no species occurs at both localities.

The marked seasonal activity of hylid frogs, especially in those areas having prolonged dry seasons, is further evidence in support of the significance of moisture to these animals. Some species transcend the moisture gradients and occur in subhumid areas as well as humid ones. For example, *Hyla microcephala* inhabits the subhumid Pacific lowlands of southern Nicaragua and northwestern Costa Rica, where its activity is restricted to the rainy months—usually May through November. Southeastward in the humid Golfo Dulce region, where abundant rain falls throughout the year, *Hyla microcephala* is active throughout the year. *Smilisca baudinii*, which also occurs in wet and subhumid environments, likewise has different periods of seasonal activity correlated with rainfall in different areas.

A definite climatic zone, characterized by cool temperatures and high humidity, occurs in the highlands of Middle America. Depending on local winds and topography, this zone usually occurs on windward slopes at elevations between about 1000 and 1800 meters. The natural climax vegetation in this zone is usually referred to as cloud forest or humid montane forest. Although rainfall is not ex-

TABLE 61  
Climatic Data for Three Stations in México.<sup>a</sup>

Station	Temperature (°C.)		Rainfall (mm.)		No. of Rainy Days		Comment
	Mean Annual	Monthly Means	Mean Annual	Monthly Means	Mean Annual	Monthly Means	
Veracruz .....	24.8	22.0-27.3	1623	7-347	119	2-20	Dry season
Huatusco .....	18.5	15.3-20.9	2078	41-386	117	2-19	No dry season
Oaxaca .....	20.2	17.9-22.4	650	2-169	84	0-16	Subhumid with dry season

<sup>a</sup> Data from Contreras Arias (1942).

cessive, the almost daily occurrence of banks of clouds maintains a high amount of atmospheric moisture and relatively little evaporation. The cool, moist conditions apparently are optimal for many amphibians, not only hylids, but also *Eleutherodactylus* and salamanders. That this abundance of frogs in the cloud forest is not associated with temperature can best be demonstrated by comparing a locality on the lowlands, a second locality in cloud forest on the adjacent slopes, and a third having nearly the same temperature, but not having clouds and high rainfall. The localities chosen for comparison are Veracruz, Huatusco, and Oaxaca in México (table 61). The dissimilarities in the hylid faunas at these three localities is more of a reflection of the amount and seasonal distribution of rainfall, rather than of temperature. Four species of hylids occur at Veracruz; two of these are among the ten species at Huatusco, but none of these species is present at Oaxaca, from which only a single species of hylid is known.

Despite the correlations existing between apparent moisture requirements and distribution of many species, certain aspects of life history are highly important in the ecological and altitudinal distribution of many hylids. This is especially noticeable in stream-breeding versus pond-breeding species, wherein the latter are excluded from many montane areas chiefly because of the absence of suitable breeding sites. Conversely, few stream-breeders descend to low elevations, because of the scarcity of the appropriate kinds of streams. Likewise, some species have developed the habit of depositing their eggs in arboreal bromeliads. The distribution of these frogs is dependent on the presence of suitable bromeliads for breeding.

DISTRIBUTION WITHIN HABITATS

The herpetological habitats (biociations) defined by Duellman (1965c, 1966c) can be used in an analysis of the ecological distribution of the 115 species of hylid frogs in Middle America. Seven major habitats are recognized; each can be defined briefly, as follows:

EVERGREEN FOREST: The humid lowland tropical forests, all frequently referred to as rain forest, are characterized by only moderate seasonal fluctuation in temperature. Although in most places definite rainy and dry seasons are evident, the habitat is at least moderately moist throughout the year. A tendency for the formation of a continuous treetop canopy provides abundant shade, which, combined with the moisture, provides a hot and humid environment. This habitat is nearly continuous on the Atlantic lowlands from southern México to central Panamá. It occurs on both Atlantic and Pacific lowlands in eastern Panamá and onto the Pacific lowlands of Colombia and northwestern Ecuador. Two isolated areas of humid tropical forest occur farther north on the Pacific lowlands (Golfo Dulce region in southeastern Costa Rica and coastal Chiapas and southwestern Guatemala).

SCRUB FOREST: The dry lowland forests can be divided into several types, known variously as thorn forest, short tree forest, and tropical deciduous forest. This habitat is characteristic of hot lowlands having a prolonged dry season. In some places the total annual rainfall is heavy, but the rainfall is concentrated in a part of the year. The remainder of the year has little or no rain. The effect of the seasonal nature of the rainfall is noticed in the deciduous nature of the vege-

tation and the marked seasonal activity of the animal life, especially the amphibians. This habitat is nearly continuous on the Pacific lowlands of México southward to the Nicoya Peninsula in Costa Rica. The Atlantic lowlands of México southward to southern Veracruz support scrub forest, which also is characteristic of the northern two-thirds of the Yucatan Peninsula and interior valleys in Chiapas, Guatemala, and Honduras.

**SAVANNA:** Scattered through the Caribbean lowlands from southern México to east-central Nicaragua is an edaphic climax vegetation consisting of grasses and scattered trees. In the north the trees are the broad-leaved nance (*Byrsonima crassifolia*); in the south pines (*Pinus caribaea*) occur. Savannas supporting scrubby trees (principally *Curatella americana*) occur on the Pacific lowlands of central Panamá and in the Valle el General in southern Costa Rica. The scarcity of shade in these savannas produces a desiccating effect on amphibians. Consequently, the amphibian life is highly seasonal and restricted to species adapted to subhumid conditions.

**CLOUD FOREST:** At elevations usually between 1000 and 2000 meters, but locally variable, on windward slopes, a distinctive vegetation formation and animal habitat occurs. This habitat, known variously as cloud forest, fog forest, or humid montane forest, characteristically is bathed in clouds nearly every day. The cool temperatures and high humidity combined with dense evergreen forest, a continuously wet mulch layer, and an abundance (at least locally) of epiphytic bromeliads, provide an apparently optimum habitat for frogs. Cloud forest is discontinuous; stands exist along the front of the Sierra Madre Oriental from Tamaulipas to northern Oaxaca, on the Pacific slopes of the Sierra Madre in Chiapas and Guatemala, in isolated patches on the seaward slopes of the Sierra Madre del Sur in Oaxaca and Guerrero, on the northern slopes of the Chiapan-Guatemalan highlands, in the highlands of central Honduras and north-central Nicaragua, in the highlands of Costa Rica and western Panamá (principally on Caribbean slopes), and on the higher ridges in eastern Panamá.

**OAK-PINE FOREST:** This usually subhumid montane habitat occurs on dry slopes in Méx-

ico and northern Central America. Usually the oak-pine association is found at elevations between 1000 and 3000 meters. It is characteristic of the major cordilleras of México and parts of the Mexican Plateau. Oak-pine forests occur as far south as northern Nicaragua; this habitat is absent in lower Central America. The open nature of the vegetation, well-drained slopes, and highly seasonal rainfall make this a suboptimal habitat for most frogs.

**PLATEAU DESERT:** The high tableland of the Mexican Plateau is characterized by fluctuating cool to warm temperatures, a small amount of seasonal rainfall, and open xerophytic vegetation. For amphibians this is a decidedly peripheral habitat inhabited by only a few species.

**ALPINE AND SUBALPINE:** At elevations usually above 2600 to 2800 meters cool, moist habitats occur. In the highlands of southern México and northern Central America fir forests occur at these high elevations. In some areas in the highlands of northern Central America a pine-cypress association or montane meadow take the place of the fir forest. A páramo-like association occurs on the highest mountains of lower Central America, such as Cerro de la Muerte and Cerro Chirripó in Costa Rica. The forests usually are moist and have deep growths of moss. Although the meadows and páramo usually receive abundant moisture, either from direct precipitation in the form of rain or snow, or from being bathed in clouds, they are subject to desiccating winds.

For purposes of analysis of the ecological distribution, these seven biociations can be reduced to five. There is nothing distinctive about the hylid fauna of the savannas; that habitat can be combined with the scrub forest into a category called dry lowland habitat. The plateau desert is nearly devoid of hylids; the only ones living there also occur in the oak-pine forest. Consequently, these two biociations are grouped into a dry montane category.

In the following list of habitats the first number is the number of species of hylid frogs known to occur in that habitat in Middle America; the number in parentheses is the number of species thought to be restricted to the habitat.



Humid Lowland . . . . .	27 (19)
Dry Lowland . . . . .	18 (15)
Humid Montane . . . . .	63 (58)
Dry Montane . . . . .	13 (11)
Alpine . . . . .	4 (2)

Only three species (*Hyla microcephala*, *H. rosenbergi*, and *Smilisca baudinii*) occur in both humid and dry lowlands. Five species (*Agalychnis annae*, *Gastrotheca ceratophrys*, *Hyla miliaria*, *Smilisca sila*, and *S. sordida*) are shared by the humid lowlands and the humid montane habitats. Two species (*Hyla euphorbiacea* and *walkeri*) are common to the dry montane and alpine habitats.

The great abundance of species in the humid habitats versus the dry ones is expected, but it is interesting to note the high degree of restriction to the dry habitats by the relatively few species that live there. Some Middle American genera (*Pachymedusa*, *Phrynosomas*, *Pternohyla*, and *Tripurion*) are so restricted. More species are found in the humid montane environments than all of the others combined. This diversity can be partly explained by the optimal amphibian habitat existing in those environments. However, the number of species in any given area is not so outstandingly large. Most of the montane hylids have very restricted geographical ranges in comparison with the lowland species.

#### ALTITUDINAL DISTRIBUTION

In Middle America hylid frogs occur at elevations from sea level to 3600 meters. The number of species is large at low elevations (0-100 meters) and then declines before greatly increasing at elevations of about 1000 meters. An abundance of species occurs at elevations of 1000 to 1500 meters, above which there is a gradual decline; only six species occur at elevations in excess of 3000 meters (fig. 319). The abundance of species at elevations of about 1000 meters is due to the overlap of many lowland and highland species at that elevation. The upper limits of distribution of 23 lowland species occur between 900 and 1200 meters, and the lower limits of distribution of 11 highland species occur at the same elevation. The altitudinal ranges of many other species extend in both

directions beyond an elevation of 1000 meters (fig. 320).

Eleven species occur exclusively at elevations of less than 500 meters. Mostly these are South American species that occur only in lower Central America. The highest elevations are attained by five species in the Mexican highlands and one in the Guatemalan highlands. The latter, *Plectrohyla glandulosa*, occurs at elevations of 3500 meters; this is exceeded only by *Hyla plicata*, which occurs at an elevation of 3600 meters in the Cordillera Volcánica in México. The other four species that occur at elevations of 3000 meters or more are: *Hyla arborescens* (3150 m.), *Hyla arenicolor* (3000 m.), *Hyla euphorbiacea* (3150 m.), and *Hyla robertsoni* (3050 m.).

Most species have altitudinal ranges of no more than 500 to 700 meters, and some, as presently known, are much more restricted. Thirty-three species have altitudinal ranges of more than 1000 but less than 1600 meters. Five other species have altitudinal ranges of more than 1600 meters; these species are (altitudinal range in parentheses): *Plectrohyla guatemalensis* (1000-2800 m.), *Hyla miotympanum* (370-2280 m.), *Smilisca baudinii* (0-1925 m.), *Hyla eximia* (900-2900 m.), and *Hyla arenicolor* (300-3000 m.). Three of these species (*Hyla arenicolor*, *Hyla miotympanum*, and *Plectrohyla guatemalensis*) are stream-breeders. Their altitudinal distributions seem to be limited primarily by the availability of suitable breeding sites; all three exist in a variety of vegetation zones. *Hyla arenicolor* is especially noteworthy in this regard; it occurs in desert, arid tropical forest, oak-pine forest, and fir forest, but always along small streams in ravines. *Hyla eximia* and *Smilisca baudinii* inhabit subhumid areas and breed in shallow temporary ponds. *Hyla eximia* lives in mesquite grassland on the Mexican Plateau and in pine forest on the plateau and surrounding mountains. It reaches its lowest altitudinal limits in the upper Balsas Basin where there is a continuity of subhumid environments from the lowlands to the plateau. *Smilisca baudinii* is widespread at low elevations and enters the highlands along subhumid corridors into intermontane valleys.

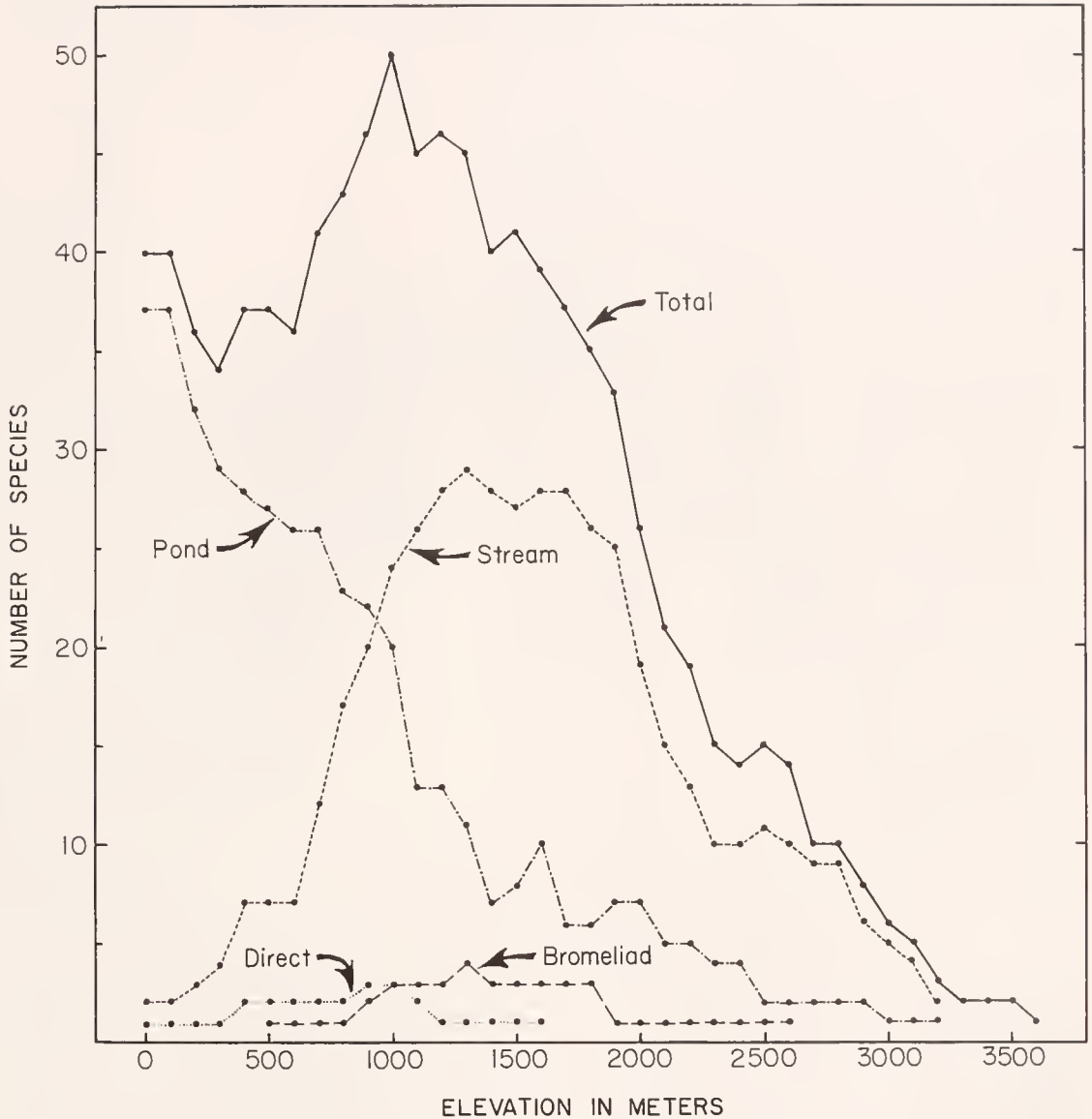


FIG. 319. Altitudinal distribution of hylid frogs in Middle America.

A distinct correlation exists between altitudinal range and mode of larval development in hylids; 31 of the 34 species that reach their upper altitudinal limits at an elevation of no more than 1000 meters are pond breeders. Forty-nine species have their lower altitudinal limits at an elevation of no more than 500 meters; 39 of these are pond-breeders; only seven stream-breeders occur at elevations below 500 meters (fig. 320). Sixty per cent of the 74 species that occur at elevations

below 1000 meters are pond-breeders, whereas only 32 per cent of the 74 species are stream-breeders. The number of pond-breeders usually is inversely proportional to the number of stream-breeders; this is not indicative of any kind of competition between the two groups but rather an expression of the availability of breeding sites (fig. 319).  
The foregoing comments on altitudinal distribution pertain to the Middle American hylid fauna as a whole. Some wide-ranging

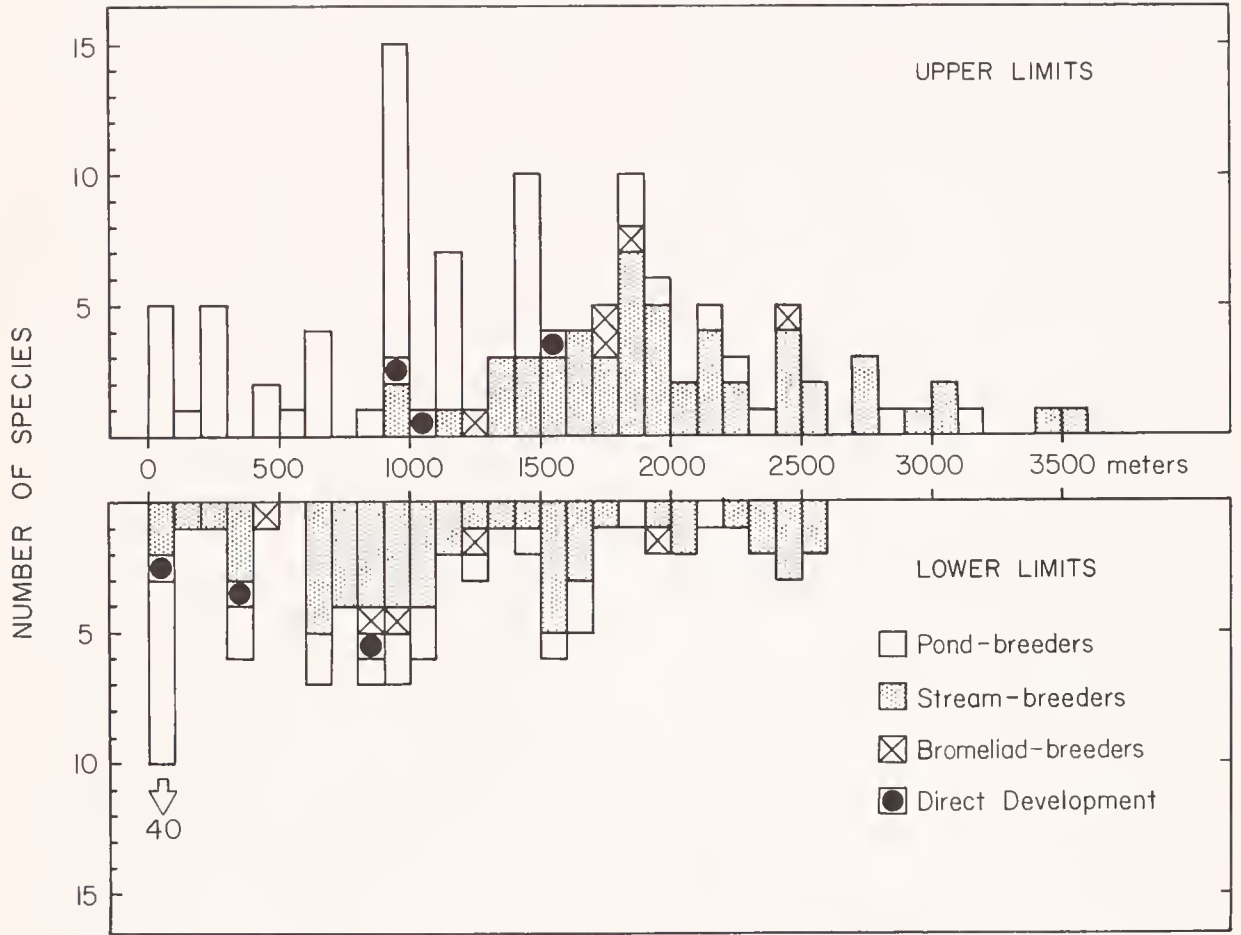


FIG. 320. Upper and lower altitudinal limits of hyloid frogs in Middle America.

species exhibit different altitudinal distributions at different latitudes. For example, *Agalychnis callidryas*, *Hyla ebraccata*, *Hyla loquax*, and *Hyla microcephala* occur only on the lowlands (elevations less than 300 meters) in southern México, whereas in Panamá and Costa Rica the altitudinal range of each of these species extends from the lowlands to elevations of more than 800 meters. *Hyla ebraccata*, *loquax*, and *microcephala* occur at elevations up to 1200 meters.

Similar variation in altitudinal distribution is exhibited by certain montane stream-breeding species that occur on both Atlantic and Pacific slopes. In nearly every species in which the altitudinal limits are well known, the altitudinal range is greater on the Atlantic than on the Pacific slopes. For example, in Oaxaca, México, *Ptychohyala leonhardschultzei*

occurs at elevations from 700 to 1850 meters on the Atlantic slopes but only from 900 to 1700 meters on the Pacific slopes. Partial altitudinal displacement occurs in *Hyla uranochroa* in the Cordillera Talamanca in Costa Rica and western Panamá where the species has an altitudinal range of 600 to 1500 meters on the Atlantic slopes and 1400 to 1720 meters on the Pacific slopes. Variation in altitudinal distribution on different slopes is primarily due to altitudinal differences in climatic zones. This is especially noticeable in the case of cloud forest, which is more restricted altitudinally on the Pacific slopes than on the Atlantic slopes.

Certain aspects of altitudinal and ecological distribution can be shown by transects across the Middle American highlands (figs. 321 and 322). In both of the transects that



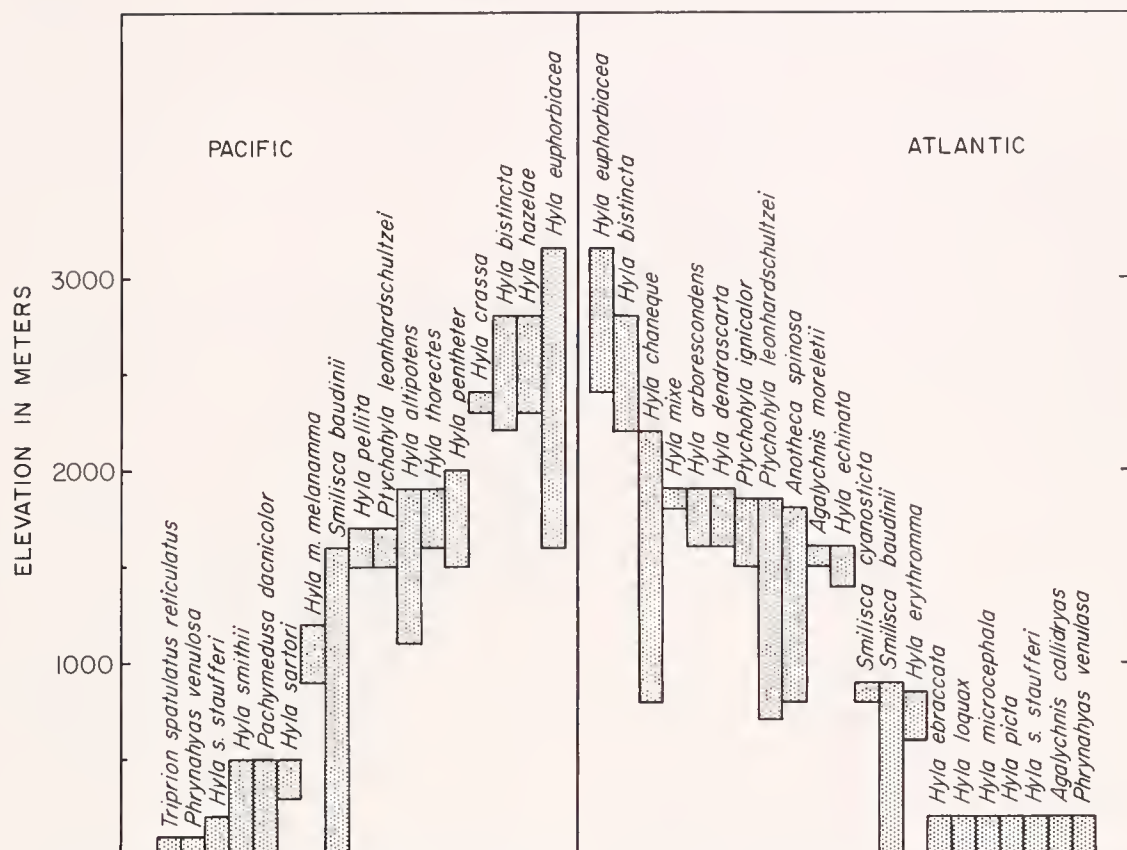


FIG. 321. Altitudinal distribution of hylid frogs on a transect across the Sierra Madre Oriental and Sierra Madre del Sur between the vicinity of Ciudad Alemán, Veracruz, and Puerto Escondido, Oaxaca, México.

are illustrated it is obvious that more species occur on the Atlantic than on the Pacific slopes. The ratio of Atlantic to Pacific slopes is 21/17 in the southern Veracruz-Oaxaca transect and 25/10 in the Costa Rican transect. In three other transects (not illustrated) the ratios are 17/12 in central Veracruz-Colima, 15/12 in Guatemala, and 18/12 in western Panamá. No more than six species or stream-breeding hylids occur at the same elevation in any of these transects. The highest species density of stream-breeders generally occurs at about the same elevation on both slopes of a given transect, but the elevation with the greatest number of stream-breeders varies latitudinally. In the Veracruz-Oaxaca transect the highest density is between 1600 and 1800 meters, and in the Guatemalan transect it is between 1400 and 1700 meters. The elevation of greatest species density of stream-breeders is between 1300 and 1400 meters in

Costa Rica and between 1000 and 1200 meters in western Panamá.

#### GEOGRAPHICAL DISTRIBUTION

The hylid fauna of Middle America presents no striking exceptions to the geographic generalities concerning the herpetofauna presented by Stuart (1957), Duellman (1966e), and Savage (1966). For convenience of discussion we can examine first the distribution in the lowlands and secondly that in the highlands.

The Middle American lowlands are most extensive on the Atlantic (Gulf and Caribbean) coasts; these lowlands generally receive more rainfall than the narrow Pacific lowlands. The Atlantic and Pacific lowlands are separated by mountain ranges, which effectively isolate populations on the lowlands of either coast, except in three areas. These areas are, from north to south: the Isthmus of

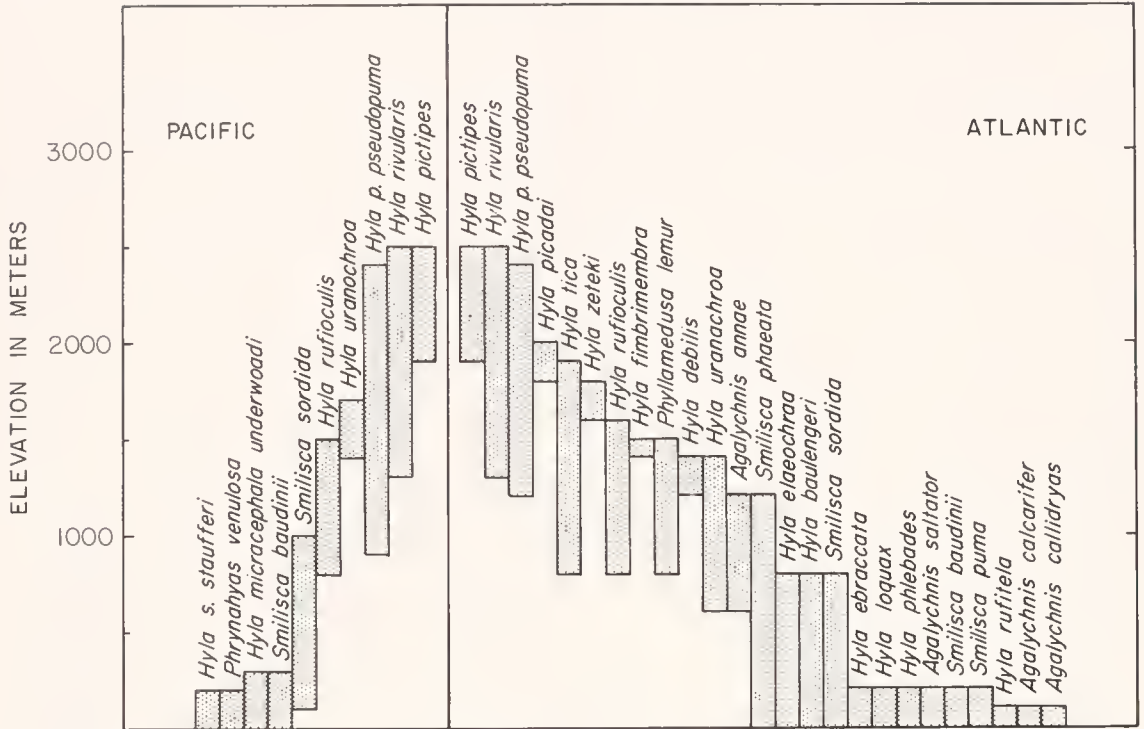


FIG. 322. Altitudinal distribution of hylid frogs on a transect across the highlands of Costa Rica, roughly from Puerto Viejo de Sarapiquí to Tárcoles.

Tehuantepec in southern México, the broad lowland continuity in Nicaragua, and the Isthmus of Panamá, which centers in the Canal Zone. The north-south lowlands are continuous on both the Atlantic and Pacific and are devoid of major physical barriers.

Examination of distribution patterns of hylids in the lowlands (species that occur on the lowlands and may or may not ascend into the foothills or mountains) reveals that there is a continuity of distribution throughout the lowlands with some species reaching either their northern or southern limits at various places, except that the ranges of several species terminate in the region of the Isthmus of Tehuantepec or in Nicaragua (fig. 323, table 62). Seven species reach their northern limits in the region of the Isthmus of Tehuantepec, and five species reach their southern limits there. Nine species reach their northern limits in either the Pacific or Atlantic lowlands of Nicaragua, and three species extend no farther south on the Atlantic lowlands. These distributions apparently are lim-

ited by environmental factors. The northern limit of tropical rainforest on the Atlantic lowlands is in southern Veracruz (northern lowlands of the Isthmus of Tehuantepec). Such typical inhabitants of rainforest as *Agalychnis callidryas*, *Hyla ebraccata*, and *Hyla loquax* extend no farther north. On the Pacific lowlands the Plains of Tehuantepec are the southern limits of the subhumid lowlands characteristic of western México. Typical inhabitants of these lowlands, such as *Hyla smithii*, *Pachymedusa dacnicolor*, and *Triprion spatulatus*, extend no farther south.

The distributional limits reached in Nicaragua are more complicated. Several species, such as *Agalychnis saltator*, *Hyla Boulengeri*, *Hyla elaeochroa*, *Hyla phlebadodes*, and *Hyla rufitela*, reach the northern limits of their distributions on the Atlantic lowlands of Nicaragua. *Hyla staufferi*, *Hyla microcephala*, and *Phrynohyas venulosa* reach their southern limits on the Atlantic lowlands of Nicaragua, but all three extend southward on the Pacific lowlands.

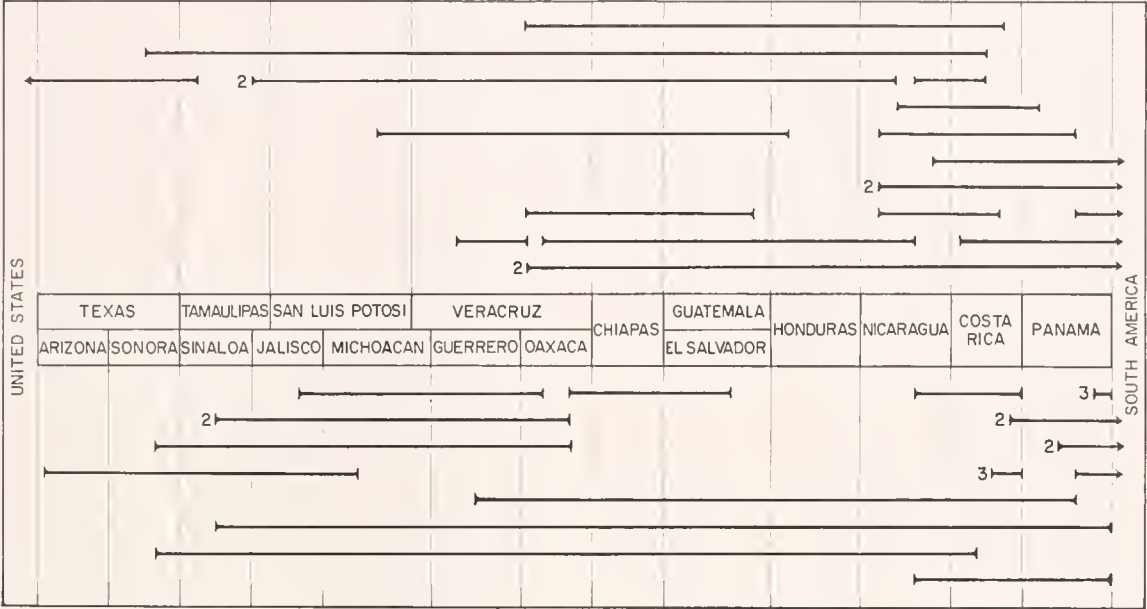


FIG. 323. Distributional patterns of hylid frogs in the lowlands of Middle America. The Atlantic lowlands are above the political units, and the Pacific lowlands are below. Each line represents one species, unless noted otherwise by a number.

TABLE 62  
Distributional Limits of Hylid Frogs in the  
Lowlands of Middle America  
(N=The Total Number of Species Present)

Region	N	Northern Limit	Southern Limit
Atlantic Lowlands			
Tamaulipas	4	2(50%)	1(25%)
San Luis Potosí	4	1(25%)	0(00%)
Veracruz	10	6(60%)	1(10%)
Guatemala	9	0(00%)	1(11%)
Honduras	8	0(00%)	1(12%)
Nicaragua	14	7(50%)	3(21%)
Costa Rica	12	1(08%)	4(33%)
Panamá	9	1(11%)	2(22%)
Pacific Lowlands			
Sonora	3	2(67%)	0(00%)
Sinaloa	6	3(50%)	0(00%)
Jalisco	7	1(14%)	0(00%)
Michoacán	7	0(00%)	1(14%)
Guerrero	7	1(14%)	0(00%)
Oaxaca	8	1(13%)	4(50%)
El Salvador	4	0(00%)	1(25%)
Nicaragua	5	2(40%)	0(00%)
Costa Rica	10	5(50%)	2(20%)
Panamá	11	6(55%)	1(09%)

The humid lowlands of the Golfo Dulce region in southeastern Costa Rica form an environmental barrier to the distribution of some species that inhabit the subhumid Pacific lowlands. *Smilisca baudinii* reaches the southern limits of its distribution in the subhumid lowlands of Costa Rica, whereas *Hyla stauferi* is present on either side of the Golfo Dulce region but is absent from the humid lowlands in the Golfo Dulce region. On the other hand, seven species (*Agalychnis callidryas*, *Agalychnis spurrelli*, *Hyla boulengeri*, *Hyla ebraecata*, *Hyla elaeochoa*, *Hyla rufitela*, and *Smilisca phaeota*) that inhabit the Caribbean lowlands of lower Central America and not the subhumid Pacific lowlands occur in the humid Golfo Dulce region. The presence of these species in the Golfo Dulce region indicates that in the not too distant past a continuous humid forested environment must have existed between the Golfo Dulce and the Caribbean lowlands. Perhaps the connection was via the Nicaraguan lowlands or maybe via the Arenal depression in the Cordillera de Tilarán in Costa Rica (Heyer, 1967).

The interesting aspects about the three lowland connections between the Atlantic and



Pacific lowlands concern the occurrence of species on one side and/or the other of each isthmus (table 63). Eleven species occur on the lowlands of the Isthmus of Tehuantepec; only two of these are found on both Atlantic and Pacific sides. However, one species (*Phrynohyas venulosa*) occurs on the Atlantic side and not on the Pacific side of the isthmus proper, but it does occur elsewhere on the Pacific lowlands. Thirteen species occur in the Nicaraguan isthmus; none is restricted to the Pacific lowlands, but two species (*Hyla microcephala* and *Hyla staufferi*) occur no farther south on the Atlantic side, and *Hyla microcephala* occurs no farther north on the Pacific side. None of the 16 species occurring in the restricted central part of the Isthmus of Panamá occurs on both coasts of the isthmus proper. However, four species that are members of the Atlantic side fauna occur in Pacific foothills to the east or west of the isthmus.

The elevations separating the Atlantic from the Pacific drainages in the isthmuses are lower than the highest elevations commonly reached by any of the species occurring in the isthmuses. Apparently no geographical barriers exist, but definite environmental differences are present between the Atlantic and Pacific lowlands in the three isthmuses. At each isthmus, the Pacific lowlands receive much less rainfall, have a longer dry season, and support less luxuriant vegetation than the Atlantic lowlands.

The distributions of most of the hylid frogs in Panamá and northwestern South America follow the cross-over pattern pointed out by Dunn (1940a), in which species that occur on the Pacific lowlands of Central America are found on the Caribbean lowlands of South America and species that occur on the Caribbean lowlands of Central America are found on the Pacific lowlands of South America. The distributional patterns are

TABLE 63  
Distribution of Hylid Frogs in Three Middle American Isthmuses

Tehuantepec	Nicaragua	Panamá
Pacific Only		
<i>Hyla smithii</i>		<i>Hyla crepitans</i>
<i>Pachymedusa dacnicolor</i>		<i>Hyla rostrata</i>
<i>Triprion spatulatus</i>		<i>Hyla microcephala</i>
		<i>Hyla roseubergi</i>
		<i>Hyla rubra</i>
		<i>Hyla staufferi</i>
		<i>Phrynohyas venulosa</i>
		<i>Smilisca sila</i>
Both Sides		
<i>Hyla staufferi</i>	<i>Hyla microcephala</i>	
<i>Smilisca baudinii</i>	<i>Hyla staufferi</i>	
	<i>Phrynohyas venulosa</i>	
	<i>Smilisca baudinii</i>	
Atlantic Only		
<i>Agalychnis callidryas</i>	<i>Agalychnis callidryas</i>	<i>Agalychnis calcarifer</i>
<i>Hyla ebraccata</i>	<i>Agalychnis saltator</i>	<i>Agalychnis callidryas</i>
<i>Hyla loquax</i>	<i>Hyla boulengeri</i>	<i>Agalychnis spurrelli</i>
<i>Hyla microcephala</i>	<i>Hyla ebraccata</i>	<i>Hyla boulengeri</i>
<i>Hyla picta</i>	<i>Hyla elaeochroa</i>	<i>Hyla ebraccata</i>
<i>Phrynohyas venulosa</i>	<i>Hyla loquax</i>	<i>Hyla phlebodes</i>
	<i>Hyla phlebodes</i>	<i>Hyla rufitela</i>
	<i>Hyla rufitela</i>	<i>Smilisca phaeota</i>
	<i>Smilisca phaeota</i>	

slightly more complicated than intimated by Dunn. Sixteen species of hylids occur in the lowlands of both Panamá and northwestern South America (table 64). Six of these show the usual cross-over pattern from Caribbean Central America to Pacific South America; seven others are on the Pacific lowlands of Central America and the Caribbean lowlands and/or the Amazon Basin of South America. Two species are principally Caribbean in Central and South America, and one occurs on the Pacific lowlands of both.

The generalities of the patterns hold true for most of northwestern South America and western Panamá. However, in eastern Panamá we find a broad zone of interdigitation and overlap of Caribbean and Pacific species. The near absence of mountain ranges of even moderate elevations and the presence of humid forests and open forest-savanna associations results in a mosaic of distributions not encountered elsewhere in lower Central America. As examples, we need only to examine the lists of species known from the lower Río Chucunaque, Darién. Four of the nine species are primarily Caribbean in Central America, whereas the other five are Pacific. Six of the thirteen species known from the Río Tuira Basin are primarily Caribbean; the other seven are typical of the Pacific lowlands in Central America.

The present distribution patterns of the hylids in eastern Panamá and adjacent Colombia seems to be primarily dependent on the distribution of environments in the region. Some species probably exist in peripheral environments and survive under suboptimal conditions. Some of these same species and some others exist in relict populations in isolated subhumid areas. The mixture of lowland species of hylids in eastern Panamá extends westward only to the Canal Zone. To the west and thence northward into Costa Rica the Caribbean and Pacific faunas are separated by high mountains. Haffer (1967a and 1967b) concluded that the distribution of birds in northwestern Colombia and adjacent Panamá also was principally governed by "forest" and "non-forest" habitats.

The highlands of Middle America are divided by lowlands into three major mountain masses, from north to south: the Mexican

highlands, the Chiapan-Guatemalan highlands, and the Costa Rican-western Panamanian highlands. The Mexican highlands are the most extensive and the highest. The great elevated area consists of the Mexican Plateau bordered on the east by the Sierra Madre Oriental, on the west by the Sierra Madre Occidental, and on the south by the Cordillera Volcánica. In addition the Sierra de Coalcomán and Sierra Madre del Sur parallel the Pacific coast in southwestern México.

The highlands of Nuclear Central America are comprised by the Sierra Madre extending from eastern Oaxaca to Honduras, the central highlands of Chiapas, the Sierra de los Cuchumatanes in western Guatemala, and a vast complex of small east-west small mountain ranges extending from Guatemala to northern Honduras.

The highlands of lower Central America are comprised principally by the Cordillera Talamanca in Costa Rica and western Panamá and the eastern extension, the Sierra de Tabasará in Panamá. The Cordillera Central and Cordillera de Guanacaste in Costa Rica complete the highland complex.

The sizes of the hylid faunas in these three highlands correlates with the size of the highland areas. Thirty-two species occur in the extensive Mexican highlands, and 21 occur in the Guatemalan highlands, whereas only 15 are found in the Costa Rican highlands. The hylid faunas of the three highlands are highly distinctive; only five species are shared between the Mexican and Guatemalan highlands, whereas one is shared between the Guatemalan and Costa Rican highlands. The genus *Plectrohyla* is endemic to the Guatemalan highlands, whereas the genus *Ptychohyla* is shared with the Mexican highlands. The *Hyla salvadorensis* group has one species in the Guatemalan highlands and one in the Costa Rican highlands.

Except for a few species that occur only on the Caribbean or Pacific slopes, the hylid fauna is rather evenly distributed throughout the highlands of Costa Rica and western Panamá. There are notable differences in the hylid faunas on the Atlantic and Pacific slopes of the Guatemalan highlands; only four species occur on both slopes. The highlands of

TABLE 64  
Distribution of Hylid Frogs in the Lowlands of Lower  
Central America and South America.

	Western Panamá		Canal Zone		Eastern Panamá		Tuira	Chocó	South America	
	Caribbean	Pacific	Caribbean	Pacific	San Blas	Bayano	Chucunaque		Caribbean	Amazon
<i>Agalychnis saltator</i>	--	--	X	--	--	--	--	X	--	--
<i>Agalychnis callidryas</i>	X	--	X	--	--	X	X	X	--	--
<i>Agalychnis spurrelli</i>	X	--	X	--	--	--	--	X	--	--
<i>Hyla boans</i>	--	--	X	--	X	--	--	X	X	X
<i>Hyla boulengeri</i>	X	--	X	X	--	--	--	X	--	--
<i>Hyla crepitans</i>	--	--	--	X	--	X	--	--	X	--
<i>Hyla ebraccata</i>	X	--	X	X	X	X	X	X	X	--
<i>Hyla microcephala</i>	--	X	--	X	--	X	X	--	X	--
<i>Hyla phlebodes</i>	X	--	X	--	--	--	X	--	--	--
<i>Hyla rosenbergi</i>	--	X	--	X	--	X	X	X	--	--
<i>Hyla rostrata</i>	--	--	--	X	X	X	--	--	X	--
<i>Hyla rubra</i>	--	--	X	X	--	X	--	--	X	X
<i>Hyla subocularis</i>	--	--	--	--	--	--	X	--	--	X
<i>Phrynohyas venulosa</i>	--	X	--	X	--	X	X	--	X	X
<i>Smilisca phaeota</i>	X	--	X	X	X	X	X	X	--	--
<i>Smilisca sila</i>	--	X	--	X	X	X	X	--	X	--



most of Honduras are too poorly known to comment on the distribution of hylids throughout those ranges.

Of the 32 species of hylids in the Mexican highlands, three wide-ranging species occur in all of the four major cordilleras, of which the Sierra Madre Occidental and Cordillera Volcánica each have four species of hylids. Fourteen species occur in the Sierra Madre del Sur; of these, six are endemic, and six are among the 23 species (14 endemic) in the Sierra Madre Oriental.

Five isolated small highland areas must be mentioned. The Sierra de los Tuxtlas in southern Veracruz has a rich hylid fauna composed mostly of species occurring either in the surrounding lowlands or on the slopes of the Sierra Madre Oriental. The Azuero highlands in the southern part of the Azuero Peninsula, Panamá, are practically devoid of hylids. Only *Smilisca sila* is a member of the depauperate fauna there. The Serranía de Darién, Serranía de Pirre, and Cerro Sapo are three separate and nearly parallel mountain ranges in eastern Panamá. *Gastrotheca nicefori* occurs on Cerro Pirre and Cerro Sapo, plus several localities in Colombia; it is the only hylid species restricted to these ranges in Central America.

The numerous continental islands along both coasts of Middle America are nearly devoid of hylid frogs. No hylids occur on the islands in the Golfo de California, Islas Tres Marias, Isla Coiba, Archipiélago las Perlas, or Archipiélago de San Blas. Two species occur on Isla Cozumel, three on Isla Grande del Maíz, one on Isla Cébaco, and four on the islands comprising the Archipiélago de Bocas del Toro.

#### EVOLUTION OF THE MIDDLE AMERICAN HYLID FAUNA

An attempt at a synthesis of the taxonomic and distributional data is a fascinating challenge. The absence of a fossil record of hylids or any group of vertebrates in Middle America makes it necessary to rely on the characters and distributions of the living species in combination with the evidence of the geological and climatic history of Middle America in order to draw zoogeographic conclusions.

The historical zoogeography of Central

America has been adequately discussed by Savage (1966) and Stuart (1966), and various regional studies in México have contributed equally substantial information (Duellman, 1960b, 1965c; Savage, 1960). Consequently, I will not elaborate on the geological history of Middle America and instead refer my readers to the above papers and the many publications cited therein.

Previous workers dealing with the history of the Middle American fauna religiously followed the Matthewsian concepts of a northern origin and southward dispersal of the families of amphibians and reptiles. Dunn (1931c) considered Central American groups that had relatives in South America to be members of his Old Northern Fauna. Schmidt (1943) called the same groups hanging relicts. Stuart (1950) recognized these Central American groups that had differentiated from their South American relatives as the Autochthonous Middle American Fauna. Savage (1966) recognized these groups as the Mesoamerican Fauna, a zoogeographical element equal in its distinctness to the Nearctic and Neotropical faunas.

Dunn and Schmidt were devoted disciples of Matthews; Stuart and Savage, although they recognized the distinctive nature of the Middle American fauna, formulated their ideas at a time when the permanence of the present continental land masses was held sacred. However, in recent years the earlier unpopular concept of continental drift has received tremendous support from the geologists who have amassed a wealth of data on paleomagnetic crustal movements, midoceanic ridges, and intercontinental continuity of beds (see Wilson, 1963; Takeuchi, Uyeda, and Kanamori, 1967; and Hurley, 1968). Suddenly Gondwanaland is in vogue. It seems that the question is not if, but when, continental drift occurred. Excellent evidence is available in support of continental connections in the Southern Hemisphere in the Paleozoic, and the early Mesozoic, and suggestive bits of evidence are present for the Jurassic and possibly early Cretaceous. Some substantial biological evidence supports the concept of Holarctic distributions (Darlington, 1965; Brundin, 1965; and Hallam, 1967). The recent work of Brundin (1967) on chironomid

midges presents a masterful synthesis of a Holantartic center of origin and dispersal. The recent find of a Triassic labyrinthodont in Antarctica (Barrett, Baillie, and Colbert, 1968) is the most significant vertebrate evidence demanding the consideration of Antarctica in the paleogeography of vertebrates. Goin and Goin recently suggested Antarctica as the center of origin of frogs.<sup>16</sup>

The time is ripe to re-examine the zoogeographic concepts that have been applied to the Middle American herpetofauna; we must now inquire about the probabilities of a northern origin and a southward dispersal versus a southern origin and a northward dispersal. We should not make the mistake that has been so prevalent in the past of assuming that the entire fauna has been derived from one direction. Instead, each group must be examined independently. What I have to say about the origin and the dispersal of the hylid fauna may or may not be applicable to other groups of organisms; that is something for other workers familiar with other groups to determine.

I recognize four principal hylid faunas in the world: 1) Neotropical—the largest and most diverse. 2) Australo-Papuan—rather large in numbers of species and moderately diverse. 3) Mesoamerican—moderately large and very diverse. 4) Holarctic—small and lacking diversity. The large number of species and incredible diversity of the South American hylids is a strong indication that the group differentiated and dispersed from that region. Only the Neotropical fauna contains all four subfamilies of hylids.

The Mesoamerican hylid fauna is distinctive but obviously related to the Neotropical fauna by virtue of the presence of three Mesoamerican autochthonous genera belonging to two subfamilies that do not occur in the Holarctic fauna. I can find no evidence to ally the Holarctic fauna with the Mesoamerican fauna. Furthermore, due to my lack of knowledge of the few Old World members of the Holarctic fauna, I have no suggestions con-

cerning the possible relationships of the Holarctic hylids with those in the Australo-Papuan region. The Holarctic hylids seem to be separate from the others. This separation is more than just spatial. Perhaps the Holarctic hylids are relatively recent forms that have yet to develop a variety of characteristics. Conversely they might be archaic forms, but due to the broad distributions of many species and the near absence of diversity the fauna probably does not possess great antiquity.

My concept of the origin of the Middle American hylid fauna centers on two invasions from Southern America and one minor invasion from North America (fig. 324). These are summarized below.

1. An invasion from South America, probably in the Cretaceous, of at least three stocks of hylids representing hylines, amphignathodontines, and phyllomedusines. This group evolved in isolation through most of the Cenozoic into the diverse Mesoamerican hylid fauna.

2. A second invasion from South America after the reformation of a land connection with Central America in the Pliocene. All species are members of the Neotropical hylid fauna.

3. A dispersal of two species groups of the Nearctic component of the Holarctic hylid fauna from North America into the highlands of northern Middle America. This probably did not occur before mid-Pliocene.

Thus, in Middle America we have three historical groups—the Mesoamerican and representatives of the Neotropical and Nearctic hylid faunas. The following discussions of the evolution of these faunas contain, I fear, as much conjecture as fact, but nothing like the tree frog witnessed by Giles (Woodhouse, 1966).

#### THE MESOAMERICAN HYLIDS

The largest historical element in the Middle American hylid fauna is the Mesoamerican element, which comprises 73 per cent of the hylid fauna in Middle America. In this element we have all of those phyletic lines that evolved in Middle America while South America was isolated by seaways during most of the Cenozoic. Included in the Meso-

<sup>16</sup> This suggestion was made in a paper entitled "Antarctica as the center of origin of frogs" presented at the annual meeting of the American Society of Ichthyologists and Herpetologists in Ann Arbor, Michigan, in June, 1968.

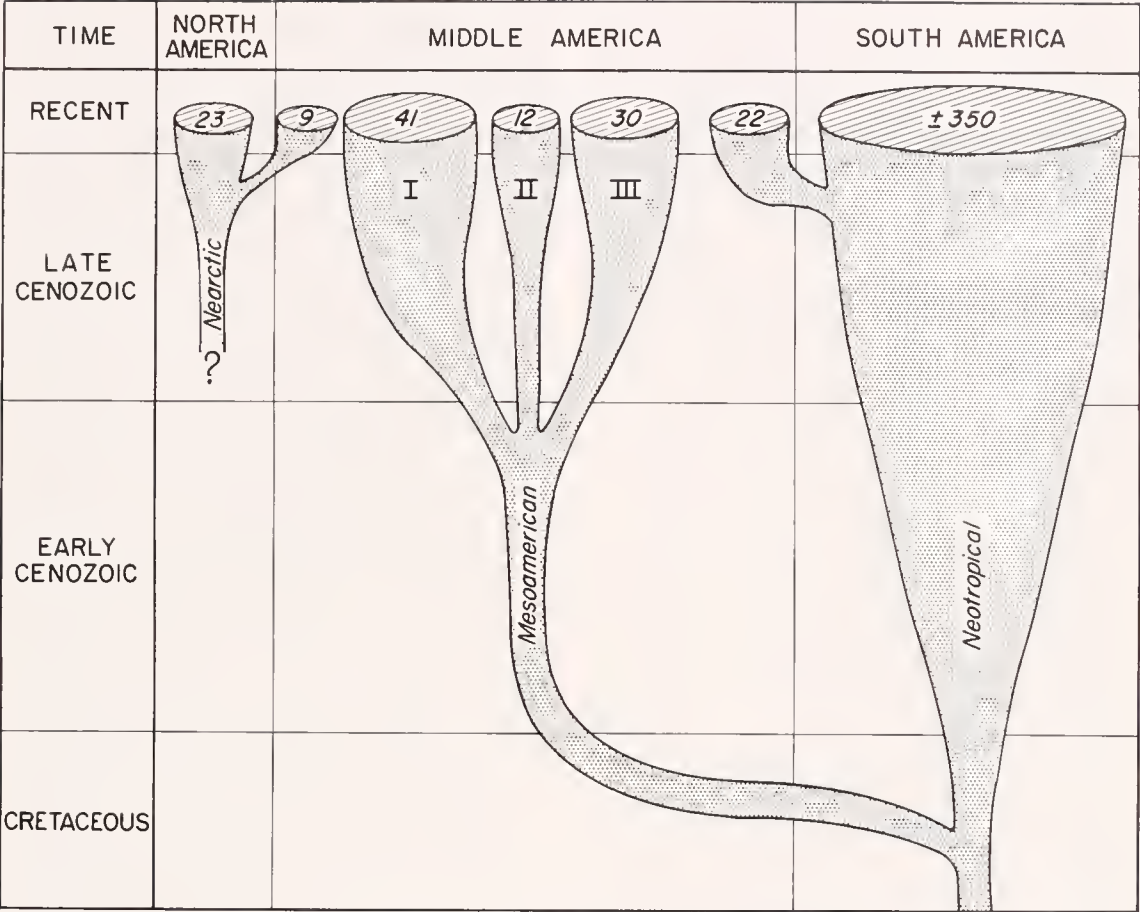


FIG. 324. Proposed phylogenetic history of the major hylid faunas in Middle America. Numbers in cones are the numbers of species. I=Nuclear Central American and Mexican Highland Component. II=Lower Central American Highland Component. III=Lowland Component.

american hylids are three components, which I refer to as: 1) the Mesoamerican Lowland Component, 2) the Lower Central American Highland Component (the Talamancan Herpetofauna of Savage, 1966), and 3) the Nuclear Central American and Mexican Highland Component (in part the Guatemalan Highland Herpetofauna of Savage, 1966). The second and third have been derived from the first, perhaps entirely independently but possibly through an intermediate form that has passed into oblivion. The all too meager evidence suggests that a basic Mesoamerican hylid fauna was composed of one phyllomedusine stock, one amphignathodontine stock and one or two hyline stocks. The two Mesoamerican highland components are quite dis-

tinct in their evolutionary histories and are discussed separately.

The stream-adapted tadpoles of the species in the two highland components are specialized derivatives of the pond-type of tadpole characteristic of the lowland component. Certain structural features of the adults also suggest that the montane species are derived from lowland types. The conclusions based on morphology are supported by the physiological work by Brattstrom (1968, p. 110), who stated: "High altitude forms [anurans] in the recent mountains of Central America are physiologically essentially lowland tropical forms that have been carried or forced into a variety of restrictive physiological plasticities."



## MESOAMERICAN LOWLAND COMPONENT:

Prior to the separation of Central America from South America in the Eocene certain groups of hylids inhabited what is now Central America; each of these groups had relatives in South America. Two of these groups (phyllomedusines and amphignathodontines) can be dispensed with readily.

The primitive phyllomedusine stock in Middle America probably was a generalized phyllomedusine, perhaps not much different from *Pachymedusa dacnicolor*. Certainly the Mesoamerican stock and the Neotropical stock which developed into *Phyllomedusa* had a walking gait and arboreal eggs. Probably a *Pachymedusa* stock was isolated on the Pacific slopes of México by the early Miocene, by which time uplift of the Mexican and Nuclear Central American highlands created increased diversity of environments. The *Pachymedusa* stock evolved towards increasing aridity, whereas the *Agalychnis* stock remained in humid forests and differentiated into six species in Middle America. The primitive *Agalychnis* stock probably was much like *Agalychnis saltator*, which evolved in the Central America peninsula south of the Nicaraguan Embayment, whereas its close ally, *callidryas* apparently developed north of the embayment. The evolution of *annae* and *moreletii* apparently are correlated with the elevation of the Talamanca range in lower Central America and the Nuclear Central American highlands, respectively. *Agalychnis spurrelli* is a specialized lowland species which probably evolved in the humid forests of lower Central America in the late Tertiary and spread into Chocoan South America and in eastern Panamá differentiated into *litoridryas*. The *Agalychnis calcarifer-craspedopus* stock migrated into South America after the Pliocene continental connection. East of the Andes the stock differentiated into *craspedopus*, whereas on the Pacific lowlands it evolved into *calcarifer*, which subsequently extended its range northward into Central America.

The Amphignathodontinae, as rather loosely defined in the present work, is represented in Middle America by one stock that was isolated there throughout the Cenozoic. This stock had certain amphignathodontine

morphological features, but lacked the brood pouch, which was developed in females in the Neotropical representatives. Thus, the only Mesoamerican amphignathodontine, *Anothea*, remained relatively primitive in its reproductive modifications. Perhaps all primitive amphignathodontines were like *Anothea* and deposited their eggs in bromeliads and/or water-filled cavities in trees.

The remaining members of the Mesoamerican lowland component are hylines currently recognized in three genera plus four species groups of *Hyla*. It is reasonable to assume one ancestral stock for all of these, except the enigmatic *Hyla miliaria* group comprising the so-called fringe-limbed tree frogs. The absence of data on life histories, mating calls, and cranial osteology for the five species placed in this group precludes any meaningful phylogenetic conclusions. I am uncertain about the five species being placed in one group. The northernmost species, *valancifer* and *cchinata*, seem to be more closely related than either is to the three southern species. Whatever their relationships might be with one another, the relationships with other hylids, either Neotropical or Mesoamerican, are even more obscure. On the basis of our present knowledge of these frogs it is not possible to determine if they originated from the common Mesoamerican stock or are representatives of a separate stock that was isolated in Middle America.

Returning now to the main hyline stock in Middle America, we have a generalized lowland pond-breeder with unspecialized tadpoles having 2/3 tooth rows. I assume that this stock had a generalized skull (quadratojugal, pterygoid-prootic articulation, and squamosal-erista parotica articulation present), teeth on the prevomers, and a frontoparietal fontanelle. Probably the members of the *Hyla godmani* group are most like this early stock. At the present time this group occurs on the Atlantic lowlands and foothills, *godmani* to the northwest of the Isthmus of Tehuantepec and *loquax* in Central America. The *Hyla picta* group seems to be closely related to the *godmani* group and to have differentiated by reduction in size, reduction of cranial elements, and modification of coloration. The two species in the *picta* group in-

habit peripheral subhumid lowlands in northern Middle America. *Hyla smithii* occurs on the Pacific lowlands of México, and *Hyla pieta* inhabits the Atlantic lowlands of México southward to northern Honduras. Their present ranges are narrowly separated by an apparent barrier—the xeric Plains of Tehuantepec. Structurally the adults of the *Hyla bromeliae* group are like those of the *pieta* group. The only major differences are in life history. The members of the *bromeliae* group deposit their eggs in bromeliads and have tadpoles with long muscular tails and ventral mouths containing two upper and four or five lower rows of teeth. This group, containing *bromeliae* in northern Central America and *dendroseartia* in southeastern México, apparently diverged from the lowland pond-breeding *pieta*-stock by adapting to arboreal breeding habits in a successful attempt to invade the foothills and low mountains, where ponds are scarce.

An early derivative from the basic Mesoamerican hylid stock is represented now by the frogs of the genus *Smilisca*, which according to Duellman and Trueb (1966) evolved in the mesic tropics of the southeastern part of the Central American paleopeninsula probably in the early Miocene, but possibly earlier. The *Smilisca*-stock differentiated into two groups—the *baudinii* group on the Caribbean lowlands and the *sordida* group on the Pacific slopes of lower Central America. Probably before the elevation of the Talamancan Range in Costa Rica and western Panamá the *sordida*-stock invaded the Caribbean of Costa Rica. One species, *puma*, evolved on the Caribbean lowlands, whereas two others, *sordida* and *sila* on the Caribbean and Pacific slopes, respectively, adapted to life in streams as the Talamancan Range uplifted in the Pliocene. The *baudinii* group of *Smilisca* remained in the lowlands of Middle America and differentiated into two species (*eyanostieta* and *phaeota*) in the humid environments, whereas *baudinii* became widely distributed in the subhumid lowlands.

Increasing aridity in the Pliocene and Pleistocene were met with some striking adaptations for survival in arid environments. According to Trueb (1970a), an apparent early divergent stock from the *Smilisca* progenitor

developed a casque head characterized by broad labial flanges and a prenasal bone. This stock evolved into *Triprion*, one species in the Yucatan Peninsula (*petasatus*) and another on the Pacific lowlands of México (*spatulatus*). Trueb (1970a) showed a progression of cranial dermal proliferation from *Smilisca baudinii* to *Pternohyla dentata* and finally *Pternohyla fodiens*, thereby demonstrating the highly probable course of evolution of *Pternohyla* from a *Smilisca baudinii*-like ancestor. *Pternohyla dentata* occurs in the Río Santiago Basin on the Mexican Plateau, and *P. fodiens*, which inhabits the lowlands of western México, extends northward into Arizona, the northernmost occurrence of any Mesoamerican hylid.

**LOWER CENTRAL AMERICAN HIGHLAND COMPONENT:** The basic Mesoamerican hyline stock provided a progenitor to the hylids of the mountains of lower Central America. This fauna consists of 12 species in five groups of *Hyla*. The primitive generalized *Hyla* in the lower Central American highlands is represented by the present-day members of the *Hyla pseudopuma* group. This group contains two species (*angustilineata* and *pseudopuma*) having generalized skulls and tadpoles that develop in montane ponds. The two species differ principally in coloration and mating call. All other species of *Hyla* in this component seem to have evolved from a *pseudopuma*-like ancestor in response to montane habitats lacking ponds for breeding. With the exception of one group of bromeliad-breeders, all of these derived species are stream-breeders and differ from one another principally in the kinds and degrees of stream adaptations of the tadpoles and progressive reduction of the skulls of the adults. The buccal adaptations of the tadpoles include enlargement of the mouth or the development of a funnel-shaped mouth but no increase in the number of tooth rows; tadpoles of all members of the lower Central American highland Component have two upper and three lower rows of teeth, except the arboreal tadpoles of the *zeteki* group, which lack definitive rows of teeth.

Although in external appearance the adults of the monotypic *Hyla lancasteri* group differ strikingly from the members of the *Hyla*

*pseudopuma* group, these differences are superficial. The only significant cranial modifications in *lancasteri* are the shortening of the snout region and reduction of the nasals. The tadpoles are moderately elongate and have only slightly enlarged mouths. The *lancasteri* group occurs at moderate elevations on the Caribbean slopes; some populations are apparently unique in the Lower Central American Highland Component by depositing their eggs on vegetation over streams.

The frogs in the *Hyla uranochroa* group (*uranochroa* and *rufiocularis*) have only slightly reduced skulls but have extremely modified stream-tadpoles, which have long muscular tails with shallow fins and funnel-shaped mouths. The frogs in this group have red eyes, a unique character in the Lower Central American Highland Component; they could have evolved from either a *pseudopuma*-like ancestor or an early *lancasteri*-like stock. Both the adults and tadpoles of *uranochroa* and *rufiocularis* are very much alike structurally; the two species probably differentiated as a result of altitudinal separation, although they now occur sympatrically at intermediate elevations on both Pacific and Caribbean slopes.

A separate adaptive line includes the stream-breeding *Hyla pictipes* and *rivularis* groups. These montane stream inhabitants are characterized by reduced cranial ossification (loss or reduction of quadratojugal, no bony articulation of the squamosal and crista parotica, and no bony connection of the medial ramus of the pterygoid with the prootic) and highly modified tadpoles having greatly enlarged ventral mouths and long muscular tails. These groups obviously are descended from a stock having a more fully developed skull and having more generalized tadpoles; thus, they probably evolved from an ancestor much like *Hyla pseudopuma*. Certainly, the *pictipes* and *rivularis* groups represent an entirely separate phyletic line from that which gave rise to the *uranochroa* group. On the basis of its somewhat more generalized skull (shorter sphenethmoid and broader frontoparietals) the monotypic *Hyla pictipes* group seems to be an early divergent line from the stock that gave rise to the *rivularis* group. *Hyla pictipes* is now restricted to high elevations in the Cordillera Central and Cordillera

Talamanca. The four species in the *Hyla rivularis* group are very similar in the structure of the adults and tadpoles. *Hyla tica* has the shortest sphenethmoid and most generalized mating call. The sphenethmoid is progressively longer in *rivularis*, *xanthosticta*, and *debilis*. The four species are partially segregated altitudinally, and no member of the group is completely geographically allopatric to all other members of the group. The four species probably differentiated through geographic and altitudinal isolation in the constantly changing cordilleras in the late Tertiary and subsequently established their present partially sympatric distributions.

Aside from the generalized *Hyla pseudopuma* group, the only members of the Lower Central American Highland Component that are not stream-breeders are the members of the *Hyla zeteki* group. The two species (*zeteki* and *picadoi*) in this group adapted to the montane forests by developing the habit of depositing their eggs in bromeliads. Because of this divergent reproductive behavior and only moderately reduced cranial elements, the progenitor of the *zeteki* group probably was a generalized pond-breeder, possibly much like the members of the *pseudopuma* group. The two species in the *zeteki* group are broadly sympatric, but *picadoi* occurs at higher elevations than *zeteki*; their differentiation may have been the result of either altitudinal isolation or geographic separation in the Cordillera Central and Cordillera Talamanca with subsequent migration of each species into the other cordillera.

It is necessary to note here that the bromeliad breeding habit apparently evolved independently in the *Hyla zeteki* and *bromeliacia* groups. The tadpoles of the former group have anterodorsal mouths and reduced tooth rows, whereas those of the *bromeliacia* group have ventral mouths and no reduction of tooth rows.

THE NUCLEAR CENTRAL AMERICAN AND MEXICAN HIGHLAND COMPONENT: In the highlands of northern Central America and in México there exists a hylid element containing 40 species currently recognized in nine species groups of *Hyla* and the genera *Plectrohyla* and *Ptychohyla*. One additional species occurs in lower Central America. All of these



groups are stream-breeders. Many members of this component have tadpoles with only slightly enlarged mouths and the basic tooth row formula of 2/3. In those tadpoles having enlarged mouths the number of tooth rows is variously increased to as many as 7/11. This is in marked contrast to the members of the Lower Central American Highland Component, in which even in those species having greatly enlarged mouths the tooth row formula is always 2/3.

One species in the foothills of lower Central America, *Hyla legleri* is closely related to the northern *Hyla salvadorensis*; by virtue of both having a tooth row formula of 2/5 these species are placed in the Nuclear Central American Component. We can assume only one other transgression of the Nicaraguan lowland gap by a member of a highland assemblage. The Guatemalan tadpole described under Species Inquirianda obviously belongs with the Lower Central American Highland Component. Like the tadpoles of the *Hyla pictipes* and *rivularis* groups, the Guatemalan tadpole has an immense ventral mouth with 2/3 tooth rows.

The combination in the same component of frogs in the highlands of Nuclear Central America with those in the highlands of México is contrary to the faunal dissimilarities of the two highland areas presented in recent summaries of the herpetofauna (Duellman, 1960b, and 1966e; Savage, 1966). Nevertheless, the Mesoamerican hylids in the two highland areas separated by the narrow lowlands of the Isthmus of Tehuantepec definitely seem to be members of one faunal element. Four species occur in both areas; members of two other species groups are found in both areas, and two closely related groups are separated geographically by the isthmus. A realistic phylogenetic history of the northern Mesoamerican highland hylids can be constructed only by taking into account the species and groups in both highland areas. Certainly the frogs in the two areas did not have entirely separate evolutionary histories.

The origin of Central American and Mexican Highland Component is obscured in the absence of any seemingly primitive type that could be intermediate between the highland component and the Mesoamerican Lowland

Component. This position is filled by the *Hyla pseudopuma* group in Lower Central American Highland Component. Consideration should be given to the one known group that spans the Nicaraguan gap and occurs in both highland areas, namely the *Hyla salvadorensis* group. The adults in this group are sufficiently generalized that they might be relatively unchanged from a progenitor of the northern highland component. However, their tadpoles are more specialized than many of those in other groups in this component, although the tadpoles in the *salvadorensis* group could have become modified after the differentiation of other groups.

We can arrive at a basic cranial type if we consider the presence of a quadratojugal, the bony articulation of the squamosal with the crista parotica, and the bony connection of the medial ramus of the pterygoid to the prootic as generalized and primitive cranial conditions. Furthermore, tadpoles that have relatively small anteroventral mouths with two upper and three lower tooth rows and rather deep caudal fins are obviously the least specialized of the stream tadpoles and are thus considered to be the generalized stream tadpoles in this component. Therefore, it seems an easy task to find the primitive group in this northern highland component; we need only to find a group having the generalized cranial and larval characters. But no such group exists, probably because the evolution of cranial features is entirely separate from the evolution of larval characters. Consequently, we have no extant group that can be considered as an idealized progenitor of the Nuclear Central American and Mexican Highland Component. Nevertheless, the frogs in this component seem to belong to a single historical group; furthermore, certain evolutionary trends and phyletic lines are evident within the group.

The five most important evolutionary trends are correlated with increased adaptation for life in and along montane streams. These trends are: 1) reduction of certain cranial elements, especially the loss of the quadratojugals (this reduction is not confined to frogs that are adapted to the stream habitat), 2) reduction and loss of vocal sacs and voice, 3) increase size of hands and length-

ening of digits, apparently as an adaptation for grasping rocks in streams, 4) depression of the body, lengthening of the tail, and reduction of the caudal fins in tadpoles, and 5) enlargement of the mouth to form a ventral oral sucker and a corresponding increase in the number of tooth rows. No one group exists that has evolved all of the above characters to their most advanced state. Several instances of parallelism are evident, such as the loss of voice in distantly related groups and the loss of the quadratojugals in two separate phyletic lines.

For the sake of simplicity the frogs in this highland component can be divided into three subcomponents. Each subcomponent represents a major phyletic line which is characterized by a combination of traits or trends not present in the other subcomponents. The first of these contains the *taeniopus*, *salvadorensis*, *erythromma*, and *pinorum* groups, a total of eight species. Most of these frogs have a well-developed quadratojugal. The *Hyla taeniopus* group, comprising three species (*chaneque*, *taeniopus*, and *altipotens*), is probably one of the most primitive groups in the subcomponent. The pterygoid is in bony contact with the prootic in all three species, and the squamosal articulates with the crista parotica in *chaneque* and *taeniopus*. A voice is present in some populations of *chaneque*; small vocal slits are present in *taeniopus* but absent in *altipotens*. The tadpoles have long muscular tails and small mouths with 2/3 (*altipotens* and *taeniopus*) or 2/4 (*chaneque*) tooth rows. *Hyla altipotens* and *taeniopus* have greatly enlarged testes; both species apparently evolved from a *chaneque*-like ancestor. The differentiation of these species seems to have been the result of geographic isolation; thus, *chaneque* evolved in the Guatemalan highlands, *taeniopus* in the Sierra Madre Oriental, and *altipotens* in the Sierra Madre del Sur. This differentiation must have occurred prior to the Wisconsin, the most recent time when cloud forest might have existed on the low ridges of the Isthmus of Tehuantepec and thereby allowed *Hyla chaneque* to cross into the Mexican highlands.

The *Hyla salvadorensis* group consists of *salvadorensis* and *legleri*; both have generalized skulls and tadpoles with 2/5 tooth rows.

Probably the ancestral stock of the *salvadorensis* group extended along the Pacific slopes of the moderately uplifted highlands from El Salvador to Costa Rica in the Pliocene; subsequently two populations were isolated by the intervening Nicaraguan lowlands in which subhumid conditions developed. The northern population evolved into *salvadorensis*, and the southern population became *legleri*.

Probably in the Pliocene a stock of small stream breeding hylids that was derived from the *salvadorensis* stock occurred on the slopes of the highlands of southern México; this stock subsequently differentiated into the *erythromma* and *pinorum* groups—the former in the Sierra Madre Oriental, and the latter in the Sierra Madre del Sur. Both groups are characterized by the loss of the pterygoid-prootic articulation and by a reduction of the quadratojugal. The tadpoles of the monotypic *erythromma* group developed 4/6 tooth rows and dispersed around the edge of the Mexican highlands; thus, it came to occur sympatrically with members of the *pinorum* group in the Sierra Madre del Sur. Prior to the Pleistocene the *pinorum* group stock invaded the Chiapan highlands to the east of the Isthmus of Tehuantepec and differentiated into *Hyla melanomma*, while the stock in the Sierra Madre del Sur evolved into *Hyla pinorum*; both species retained the 2/5 tooth formula of the ancestral *salvadorensis* group. No later than Wisconsin time, *melanomma* invaded the Sierra Madre del Sur, where it occurs sympatrically with *pinorum*. Perhaps *melanomma* and *pinorum* differentiated in different areas in the Sierra Madre del Sur, and subsequent to their differentiation *melanomma* crossed the Isthmus of Tehuantepec to the Chiapan highlands.

The second subcomponent contains four groups of *Hyla* and the genus *Ptychohyla*, a total of 15 species. All of these frogs lack a quadratojugal and a bony articulation of the pterygoid with the prootic. Only in the most primitive *Hyla miotympanum* group does the squamosal have a bony articulation with the crista parotica. The differentiation in this group evidently was correlated with, or occurred subsequent to, the first major uplift of the highlands in the Miocene. The *Hyla*

*miotympanum* group consists of two species (*miotympanum* and *arborescendens*); the former occurs at lower elevations in the Sierra Madre Oriental and has tadpoles with 2/3 tooth rows, whereas the latter lives at higher elevations in the same mountains and has tadpoles with 2/4 tooth rows. The species probably differentiated at different elevations; the tadpoles of *arborescendens* with their longer tails and larger mouths having more tooth rows reflect adaptation to the more swift streams typical of higher elevations. The two species in the *Hyla hazelae* group (*hazelae* and *thorectes*) retained the generalized stream tadpoles of the *miotympanum* group, but lost the bony articulation between the squamosal and crista parotica. The *hazelae* group probably is a relatively recent divergent line from the *miotympanum* group. Possibly the members of the *hazelae* group are relicts of a former more widespread *miotympanum* group that were isolated in separate highland areas due to increasing aridity in post-Wisconsin time.

The *Hyla mixomaculata* and *sumichrasti* groups are the most specialized members of the second subcomponent. Both have reduced cranial elements; tadpoles of the former group have 7/11 tooth rows, and tadpoles of the *sumichrasti* group have 3/7 tooth rows. Members of the *mixomaculata* group apparently lack a voice. Present distributional evidence suggests that the *mixomaculata* group originated in the Sierra Madre Oriental and that the *sumichrasti* group originated on the Pacific slopes of México. Each group probably evolved independently from a generalized ancestral stock, possibly the progenitor of the *miotympanum* group. A *mixomaculata*-like stock apparently spread southward into the Sierra Madre del Sur and there gave rise to *pellita*, whereas the population that remained in the Sierra Madre Oriental evolved into *mixomaculata*. *Hyla mixe* and *nubicola* seem to be closely related derivatives of the *mixomaculata*-like stock. They presumably arose as isolates in the Sierra Madre Oriental, perhaps during climatic fluctuation in the Pleistocene.

The last group in the second subcomponent is the genus *Ptychohyla*, an assemblage of five species differing from all other Middle

American hylids by having large ventrolateral glands in the breeding males. The genus contains two species groups differing in larval, adult, and ethological characters. Duellman (1963e) suggested that *Ptychohyla* was related to the *Hyla uranochroa* group in lower Central America. Now that the stream hylids of Middle America are better known such an arrangement does not seem to be so plausible, although tadpoles with funnel-shaped mouths occur in *Ptychohyla* and in the *Hyla uranochroa* group. Perhaps *Ptychohyla* evolved from a generalized *Hyla miotympanum*-like stock in the Guatemalan highlands. There the stock differentiated into two groups, probably by means of selection for larval differences. This differentiation must have occurred by mid-Pliocene, after which time the continued uplift of the Guatemalan highlands separated the *Ptychohyla euthysanota* stock into *euthysanota* on the Pacific slopes and a *spinipollex-leonhardschultzei* stock on the Atlantic slopes. The latter stock crossed the Isthmus of Tehuantepec in a glacial period of the Pleistocene and differentiated into *leonhardschultzei* in the Mexican highlands, whereas the residual stock in Guatemala developed into *spinipollex*. The *schmidtorum* group also crossed the isthmus and developed into *ignicolor* in the Mexican highlands; at the same time the Guatemalan population evolved into *schmidtorum*.

The third subcomponent contains the *Hyla distincta* group (nine species) and *Plectrohyla* (10 species). These two groups exhibit parallel progressive adaptations to the mountain stream habitat; on the basis of their similar morphology, they must be closely related. In both groups the skulls are well ossified, but the quadratojugal is greatly reduced or absent. Species in both groups have blunt heads and large hands with long fingers. Although the tadpoles have long muscular tails they have only slightly enlarged ventral mouths with two upper and three lower tooth rows. The advanced species in both groups lack a voice. Probably the ancestral stock to these two groups was widespread in the moderately uplifted highlands of southern México and Guatemala in the Miocene. Subsequently, great uplift of the highlands in the Pliocene resulted in the isolation of the an-



cestral *Plectrohyla* in the Chiapan-Guatemalan highlands and the *Hyla bistincta* stock in the Mexican highlands.

The *bistincta* group is nicely divided into three subgroups—two generalized species (*bistincta* and *pentheter*) having vocal slits and unspecialized hands, two related divergent species (*chryses* and *charadricola*), and five related allopatric specialized species (*robertsorum*, *pachyderma*, *siopela*, *crassa*, and *bogertae*). The primitive member of the group, *Hyla bistincta*, is widespread in the Mexican highlands. The closely related *Hyla pentheter* probably evolved in the Sierra Madre del Sur from the widespread *bistincta* stock, which also differentiated into a more specialized form in the high mountains of the Sierra Madre Oriental. The latter stock probably was continuously distributed through those mountains in pluvial periods in the Pleistocene, but now is represented only by relict populations that have differentiated sufficiently to be considered as five allopatric species. From north to south these species are *robertsorum*, *pachyderma*, *siopela*, *crassa*, and *bogertae*. *Hyla chryses* and *charadricola* also probably represent relicts of a former widespread derivative of the *Hyla bistincta*-like stock, but their relationships with *bistincta* and *pentheter* are not clear.

Concomitantly with the diversification of the *Hyla bistincta* group in the Mexican highlands, *Plectrohyla* was differentiating in the Chiapan-Guatemalan highlands. Conceivably, in the course of the uplift in the Pliocene the *Plectrohyla* stock was separated into a highland component and another component at moderate elevations on the slopes. The latter component retained vocal slits and evolved into a group of small species, whereas the highland component evolved into a group of larger species lacking vocal slits.

The former group, which for convenience can be called the *sagorum* group, eventually established populations on the Atlantic and Pacific slopes of the highlands. Possibly, the species now known as *quecchi* was the original inhabitant on the Atlantic slopes, whereas *matudai* was endemic to the Pacific slopes. Through isolation, differences in voice, shape of the snout, and mouthparts of the tadpoles developed. Subsequent climatic fluctu-

ation, probably in the Pleistocene, permitted migration southward of the *quecchi*-stock and northward of the *matudai*-stock. Depression of climatic zones and uplift through volcanism again resulted in isolation of populations on Atlantic and Pacific slopes, but this time two species were present on each slope. The *matudai*-stock on the Atlantic slope differentiated into *ixil*, and the *quecchi*-stock on the Pacific slope evolved into *sagorum*.

The relationships of the species in the highland component (*guatemalensis* group) are more obscure. *Plectrohyla glandulosa* and *pynochila* seem to be the least specialized species; the condition of the prepollical process in these species probably is relatively unchanged from that of the *Plectrohyla* prototype and is much like that in the *Hyla bistincta* group. It is possible that *glandulosa* developed in the Sierra de los Cuchumantanes in Guatemala, while *pynochila* was isolated in the highlands of central Chiapas. Apparently *Plectrohyla avia* represents an evolutionary intermediary between the generalized *glandulosa*-*pynochila* stock and *guatemalensis* and *hartwegi*. The prepollical spine is long and pointed in *avia* (independently evolved in the *sagorum* group) and is bifid in *guatemalensis* and *hartwegi*. *Plectrohyla avia* is endemic to moderately high elevations on the Pacific slopes; *hartwegi* occurs at the same elevations but farther west. *Plectrohyla guatemalensis* occurs nearly throughout the geographical (but not the altitudinal) range of the genus. It occurs sympatrically with *avia* and possibly with *hartwegi*.

#### THE NEOTROPICAL HYLIDS

All four subfamilies of hylid frogs have their greatest diversity in South America. With the exception of the Hylinæ, only two genera (*Anotheca* and *Pachymedusa*) are entirely extra-Neotropical. As can be expected in any large fauna such as the Neotropical hylids, there are many diverse types of morphological, developmental, and behavioral adaptations. Some of the adaptations that are characteristically Neotropical and not present in Mesoamerican groups are summarized below.

1. Phyllomedusines having grasping feet (*Phyllomedusa*).

2. Triangular dermal helmet (hemiphractines).

3. Amphignathodontines carrying eggs on the back or in a dorsal pouch (*Amphignathodon*, *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, *Nyctimantis*, and *Stefania*).

4. Paired lateral vocal sacs behind the angles of the jaws (*Osteocephalus*, *Phrynohyas*, *Argenteohyla*, and *Trachycephalus*).

5. Odontoids on mandible, palatine, and parasphenoid (*Phyllodytes*).

6. Single, median, subgular vocal sac formed by longitudinal dermal folds on throat (*Sphaenorhynchus*).

7. *Hyla* having angular prevomerine denticulous processes, such as are characteristic of members of the *albomarginata*, *boans*, *geographica*, and *lanceiformis* groups.

8. *Hyla* having projecting snouts and reduced webbing between the first and second toes (*rubra* group).

9. *Hyla* having pelagic tadpoles with 2/4 tooth rows (*albomarginata* and *boans* groups).

10. *Hyla* having tadpoles with xiphicereal tails and terminal mouths lacking teeth, such as are characteristic of members of the *leucophyllata*, *microcephala*, and *parviceps* groups.

11. Haploid number of 15 chromosomes (*leucophyllata*, *microcephala*, and *parviceps* groups); the same number occurs in the Papuan *Hyla angiana*.

The above features, taken together or individually, characterize hylid frogs that underwent their diversification in South America. Much, if not all, of this diversification probably occurred during the period of the Cenozoic (Paleocene-Pliocene) when South America was isolated from Central America by seaways.

Subsequent to the connection of Central America with South America in the late Pliocene, members of several different phyletic lines of the diverse Neotropical hylid fauna invaded Central America. It is possible that some of these immigrants arrived somewhat earlier by means of island-hopping through the archipelago existing in the Cenozoic Panamanian Portal. However, hylids seem to be notoriously poor at this means of dispersal,

as witnessed by the poverty of the West Indian species of hylids in comparison with the exceedingly rich *Eleutherodactylus* fauna there. It is not necessary to assume immigration of the Neotropical hylids into Central America prior to the continental connection, because the distribution and minor differentiation of this fauna in Central America can be explained adequately on the basis of the later arrival.

The Neotropical hylid fauna in Central America consists of 22 species. Four of these species occur only in lower Central America and at present are not known from South America, although in each case a closely related, and possibly conspecific, taxon is known in South America. *Phyllomedusa lemur* in Costa Rica and Panamá is closely related to *P. buckleyi* and *medinae* in South America. *Phyllomedusa venusta*, which is known from only one locality in eastern Panamá, is remarkably similar to *P. edentula* in Amazonian South America. *Hemiphractus panamensis* is very much like the Ecuadorian *H. fasciatus*; acquisition of material from Colombia should show that both nominal species belong in the same taxon. The relationships of the Panamanian *Gastrotheca ceratophrys* are with the Chocoan *G. cornutum*, which might be conspecific.

Most of the other species are more widely distributed in Middle America (table 65). Species in four groups have undergone differentiation in Middle America. *Hyla ebraccata*, the only Middle American species in the large Amazonian *Hyla leucophyllata* group, barely enters South America in Pacific Colombia. *Hyla rufitela* is a Middle American endemic and northernmost member of the South American *Hyla albomarginata* group. Five of the 25 species of the Neotropical *Hyla rubra* group occur in Middle America; two of these species (*elaeochroa*, *staufferi*) apparently differentiated in Central America and are restricted to Middle America. The Neotropical *Hyla microcephala* group is composed of about a dozen species, four of which occur in Middle America. Evidently the Middle America members of this group differentiated from a single stock. Two of the resulting species (*robertmertensi* and *sartori*) are restricted to Middle America; *phlebodes* barely

TABLE 65  
Distribution of Species of Neotropical Hyliid Groups in Middle America

Species	South America	Eastern Panamá	Western Panamá	Costa Rica	Nicaragua- Honduras	Guatemala- Chiapas	Eastern México	Western México
<i>Phyllomedusa lemur</i> .....	?	X	X	X	--	--	--	--
<i>Phyllomedusa venusta</i> .....	?	X	--	--	--	--	--	--
<i>Hemiphractus panamensis</i> .....	?	X	X	--	--	--	--	--
<i>Gastrotheca ceratophrys</i> .....	?	X	X	--	--	--	--	--
<i>Gastrotheca nicefori</i> .....	X	X	--	--	--	--	--	--
<i>Phrynohyas venulosa</i> .....	X	X	X	X	X	X	X	X
<i>Hyla rubra</i> .....	X	X	--	--	--	--	--	--
<i>Hyla elaeoehroa</i> .....	--	--	X	X	X	--	--	--
<i>Hyla staufferi</i> .....	--	--	X	X	X	X	X	X
<i>Hyla boulengeri</i> .....	X	X	X	X	X	--	--	--
<i>Hyla rostrata</i> .....	X	X	--	--	--	--	--	--
<i>Hyla microcephala</i> .....	X	X	X	X	X	X	X	--
<i>Hyla robertmertensi</i> .....	--	--	--	--	--	X	--	--
<i>Hyla phlebodes</i> .....	X	X	X	X	X	--	--	--
<i>Hyla sartori</i> .....	--	--	--	--	--	--	--	X
<i>Hyla ebraecata</i> .....	X	X	X	X	X	X	X	--
<i>Hyla subocularis</i> .....	X	X	--	--	--	--	--	--
<i>Hyla rufitela</i> .....	--	X	X	X	X	--	--	--
<i>Hyla erepitanus</i> .....	X	X	--	--	X	--	--	--
<i>Hyla rosenbergi</i> .....	X	X	X	X	--	--	--	--
<i>Hyla boans</i> .....	X	X	--	--	--	--	--	--
<i>Hyla eolymba</i> .....	X	X	X	X	--	--	--	--

<sup>a</sup> ? indicates the presence of closely related, possibly conspecific species in South America.

enters South America, and *microcephala* is widespread in South and Middle America.

The relationships of the montane, stream-breeding *Hyla colymba* are with three Andean stream-breeding species comprising the *Hyla bogotensis* group. Apparently *Hyla colymba* immigrated into Central America from South America after the closure of the Panamanian portal in the late Pliocene.

The Neotropical hylid fauna in Central America apparently became established there after 16 separate phyletic lines entered Central America from South America. The evolution of these separate phyletic lines took place in South America prior to the immigration of members of these groups into Central America. If my earlier suppositions about the relationships of the Central American *Phyllomedusa*, *Hemiphractus*, and *Gastrotheca* are correct, differentiation in Middle America has

taken place in only five of the 16 groups. The immigrations are summarized below:

1. *Phyllomedusa buckleyi-medinae-lemur* series from Amazonian South America to foothills of lower Central America.
2. *Phyllomedusa edentula-venusta* from Amazonian South America into Panamá.
3. *Hemiphractus fasciatus-panamensis* probably from Amazonian South America into Chocoan region and Panamá.
4. *Gastrotheca cornutum-ceratophrys* from Chocoan South America into Panamá.
5. *Gastrotheca nicefori* from the Andes to mountains of eastern Panamá.
6. *Phrynohyas venulosa* from non-forested lowlands east of the Andes into lowlands of Middle America.
7. *Hyla rubra* group (*boulengeri*-like stock) from Amazonian lowlands into Central America; subsequent differentiation of



*rostrata* and migration of *rostrata* into non-forested lowlands of northern South America.

8. *Hyla rubra* group (*rubra-clacochroa-staufferi* stock) from Amazonian South America into Central America; subsequent differentiation of *elaeochroa* and *staufferi* from *rubra*.

9. *Hyla microcephala*-like stock from Amazonian South America; subsequent differentiation of *phlebodes*, *sartori*, and *robertmertensi* from *microcephala*, of which *phlebodes* extended its range into Chocoan South America.

10. *Hyla leucophyllata*-like stock from Amazonian South America; subsequent differentiation of Middle American populations into *ebraccata*, which extended its range into Chocoan Colombia.

11. *Hyla subocularis* from Amazonian South America into eastern Panamá.

12. *Hyla crepitans* from non-forested areas of northern South America into eastern Panamá and subsequently to northern Honduras.

13. *Hyla rosenbergi* from Chocoan South America into lower Central America, or from a *boans*-like stock from Amazonian South America with subsequent differentiation into *rosenbergi* in lower Central America followed by migration into Chocoan South America.

14. *Hyla boans* from Amazonian South America into eastern Panamá.

15. *Hyla albomarginata*-like stock from Amazonian South America into lower Central America; subsequent differentiation of Central American populations into *rufitela*.

16. *Hyla colymba* from Andean foothills into mountains of lower Central America.

The temporal sequence of these invasions is shrouded by our lack of knowledge of the climatic history of the isthmian link. But even so, some temporal arrangements seem to be rather obvious. A relatively early invasion can be postulated for those groups that have undergone differentiation in Central America and/or have migrated into northern Middle America. Those species that have not differentiated from South American populations and have restricted ranges in lower Central America could have entered Central America at a later time. I conceive of five temporal invasions; these are not thought to be completely distinct "faunal waves" but rather as

the approximate temporal sequence of invasion.

Probably the earliest members of the Neotropical hylid fauna to enter Middle America were the *Hyla microcephala*, *rubra*, and *boulengeri* stocks, all of which subsequently differentiated into several species in Middle America. Perhaps at about the same time, *Phrynohyas ventulosa* entered Middle America. Some members of all these groups inhabit the subhumid lowlands of Middle America, all of these groups have dispersed northward into México. I consider that this first invasion of Neotropical frogs took place soon after the closure of the Panamanian Portal in the late Pliocene. If any of the Neotropical hylids reached Central America by island-hopping prior to the closure of the portal, they certainly must have been members of these groups.

The *Hyla albomarginata* and *leucophyllata* groups and *Hyla crepitans* could have entered Central America somewhat later, possibly at the end of the Pliocene or in early Pleistocene time. The first two groups differentiated from their parental Neotropical stocks and dispersed through humid lowland forests of lower Central America; both reached the Golfo Dulce region of the Pacific lowlands. *Hyla ebraccata* (the Middle American derivative of the *leucophyllata* group) subsequently extended its range to southern México and northwestern South America. The Middle American *Hyla crepitans* is undifferentiated from the populations in northern South America, but it has existed in Central America for a sufficient length of time to extend its range from the subhumid savannas of Panamá to the subhumid lowlands of northern Honduras without leaving any relict populations in the intervening lowlands now covered mostly with humid forest. This feat also was accomplished by *Cnemidophorus lemniscatus*.

A third group of Neotropical species apparently entered Central America during a Pleistocene glacial period when temperatures were depressed and probably some lowland areas had more rainfall than they do now. All of the species in this group (*Phyllomedusa lemur*, *Hemiphractus panamensis*, *Gastrotheca ceratophrys*, *G. nicefori*, and *Hyla colymba*) live in humid foothill forests, and

none has greatly differentiated in Central America. Two species (*Phyllomedusa lemur* and *Hyla colymba*) extend to Costa Rica; the others are restricted to Panamá and Colombia.

*Phyllomedusa venusta*, *Hyla boans*, and *H. subocularis* barely enter Central America in eastern Panamá; each species is a member of a widespread group in Amazonian South America. They are the most recent immigrants.

In Middle America the Neotropical hylids are principally lowland in their distribution. Neotropical species comprise 70 per cent of the 16 species of hylids in the Canal Zone, but only 40 per cent of the 13 species on the Caribbean lowlands of Costa Rica and only 37 per cent of the eight species in the lowlands of southern Veraacruz, México. Five of the Neotropical hylids live in foothills or low mountains in Central America. Three of these are only in Panamá; two also occur in Costa Rica, and none is a part of the rich highland hylid fauna in Nuclear Central America and México.

The relative paucity of Neotropical hylids in the lowlands of northern Middle America and their absence in most of the highland regions can be explained on the bases of time, lack of adaptations to environmental conditions, and competitive factors. Some of the earlier invaders, such as *Hyla staufferi* and *Phrynohyas venulosa*, which are adapted to subhumid environments, have migrated northward to the northern limits of the tropics in México. Subhumid conditions seem to be a controlling factor to the dispersal of some lowland species, such as *Hyla ebraccata*, *elaeochroa*, and *rufitela*, although *elaeochroa* and *rufitela* do not seem to have reached their potential northern limits of distribution, possibly due to lack of time. There are no obvious ecological or physical barriers at the presently known limits of distribution of *Gastrotheca ceratophrys* and *Hemiphractus panamensis* in Central America. Again, perhaps only more time is required for them to extend their ranges along the foothills of the Cordillera Talamanca and Cordillera Central of Costa Rica, unless, of course, they already exist there and have not been found by the many collectors who have swarmed over Costa Rica in the last decade.

The extensive Middle American highlands are devoid of Neotropical hylids save *Hyla colymba*, the only Neotropical stream-breeder in Central America. The absence of suitable breeding sites for the pond-breeding Neotropical hylids in the mountains of Middle America is an important limiting factor to those species. I can find no evidence that any of the many groups of montane stream-breeding hylids in Middle America descended from a Neotropical stock. This absence of stream descendants from Neotropical lines is striking in comparison with the multitudinous stream-inhabitants that seemingly descended from Mesoamerican lowland pond-breeders. Although lack of time and presence of competitors may be of some importance, I think that the absence of evolutionary potential in the Neotropical pond-breeders precludes their diversification into montane habitats in Central America. With the exception of the members of the *Hyla rubra*, and *albomarginata* groups, all of the Neotropical lowland pond-breeders in Middle America have either specialized breeding behavior for ponds (*boans* group) or specialized pelagic tadpoles (*leucophyllata*, *microcephala*, and *parviceps* groups). In fact, the tadpoles of none of the Neotropical groups is sufficiently generalized to adapt to stream conditions.

Competition may be an important factor in the distribution and relative abundance of Neotropical versus Mesoamerican species in the Middle American lowlands, especially the extensive subhumid areas, characterized by prolonged dry seasons. Adaptations by Mesoamerican hylids for survival under these severe environmental conditions include surface-film eggs (*Smilisca*), integumentary-cranial co-ossification (*Pternohyla* and *Triprion*), and rapid development of tadpoles (all three genera mentioned). Among the Neotropical species in Middle America, only *Phrynohyas venulosa* has corresponding adaptations (surface-film eggs, rapid tadpole development, and thick glandular skin).

Even though the Neotropical species comprise only 19 per cent of the total Middle American hylid fauna, these groups form a significant part of the fauna in lower Central America. Some Neotropical species have spread throughout the lowlands of Middle

America, but the Neotropical hylids have had only moderate success in the highlands of lower Central America and are absent from the highlands north of Costa Rica.

#### THE NEARCTIC HYLIDS

In comparison with the Neotropical and Mesoamerican elements, the Nearctic hylid fauna is characterized by a paucity of species and little diversity. In the present systematic arrangement 26 species are grouped in four genera, the largest of which is *Hyla* with 16 species in four groups. *Pseudacris* (seven species) and *Limnaeodius* (one species) are weakly differentiated from *Hyla*. However, Chantell (1968) suggested that *Limnaeodius* might be more closely related to *Acris*. The two species in the latter genus are notably distinct from other Nearctic hylids.

Although there are fragmentary fossil remains from various parts of North America from the Lower Miocene through the Pleistocene (see Auffenberg, 1956; Chantell, 1964; Holman, 1959, 1961, 1962, 1963, "1966" [1968], 1967; Lynch, 1964, 1965b, 1966c; and Tihen, 1960), none of these fossils contributes significantly in unraveling the systematic and zoogeographic relationships of the Nearctic hylids, neither among the groups recognized in North America nor with the Mesoamerican hylids. A possible minor exception is the Upper Miocene-Lower Pliocene *Pseudacris nordensis* from Nebraska, Chantell (1964) suggested that this species might be intermediate between *Hyla* and *Pseudacris*, although he found material referable to *Pseudacris clarkii* in the same fauna.

No workers have successfully related Nearctic species to members of the Mesoamerican hylid fauna. Blair ("1958" [1959] and 1960) placed *Smilisca baudinii* in the *Hyla versicolor* group and *Hyla stauferi* in the *Hyla eximia* group. These erroneous groupings were based solely on similarities of the mating calls of *baudinii*, *stauferi*, and Nearctic species without consideration of the mating calls of the Mesoamerican relatives of *baudinii* and *stauferi*; furthermore, morphological characters were not considered. Several authors have suggested that frogs in the *Hyla eximia* group are closely related to the *Hyla arborea* complex in Eurasia; the most recent

statement is by Taylor (1962, p. 346): "The *arborea* group of *Hyla* also occurs in America. A species group in México (including *euphorbiacea*, *cardenasi*, *eximia*, *arboricola*, *lafrentzi*, and *wrightorum*) must be regarded as members of the *arborea* group. Some populations of *arborea* are so similar to *lafrentzi* that they can be separated only with considerable difficulty, if at all."

The relationships of the Nearctic hylids presumably are with the Palearctic species. Anthony Gaudin is currently investigating the osteological characters of the Holarctic hylids. When his work is completed, and the results are compared with osteological data on the Mesoamerican hylids, a convincing argument might be put forth for the distant relationships of the Nearctic and Mesoamerican hylids. On the basis of the present evidence I can only assume such a relationship.

*Acris* and *Pseudacris* barely enter northern México and would not be included in an account of Middle American hylids were it not for the fact that the Mexican-United States boundary is the arbitrary northern limit for this study.

The Nearctic species of *Hyla* can be placed in four groups. The monotypic *Hyla crucifer* group and the *Hyla cinerea* group (*cinerea* and *gratiosa*) are confined to eastern North America. The *Hyla versicolor* group (*arenicolor*, *versicolor*, *chrysoscelis*, *avivoca*, and *femoralis*) is widespread east of the Sierra Nevada in the United States. *Hyla arenicolor* is the westernmost member of the *Hyla versicolor* group; it dispersed southward on the Mexican Plateau probably in pluvial periods in the late Pleistocene and post-Wisconsin.

The only other Nearctic group in Middle America is the *Hyla eximia* group, represented by the wide-ranging, variable *Hyla regilla* in western North America, probably *Hyla squirella* in southeastern North America, possibly *Hyla andersonii* in eastern United States, and five species (*cadaverina*, *plicata*, *eximia*, *euphorbiacea*, and *walkeri*) that inhabit México. I agree with Jameson, Mackey, and Richmond (1966) that the *eximia* group (their *Hyla regilla* stock) was more widespread in pluvial (glacial) periods of the Pleistocene. However, those authors were working under the erroneous assumption that *plicata* (their



*lafrentzi*) and the northern populations of *eximia* (their *wrightorum*) were conspecific with *regilla*. Moreover, they did not consider the two southern species (*euphorbiacea* and *walkeri*).

The dispersal and subsequent differentiation of the *eximia* group in western North America and in México is correlated with the Madre-Tertiary Geoflora (Peabody and Savage, 1958). The historical components of southwestern North America include a Madrean Complex of the Young Northern Element (Savage, 1960). The *Hyla eximia* group, in México at least, is part of the Madrean Complex. Apparently an early *eximia* group-stock was present in the Mexican highlands in the Pliocene. Uplift of the Cordillera Volcánica in the Pliocene probably tended to isolate montane populations of a former more widespread stock; these montane isolates are known today as *Hyla plicata*. This same uplift also isolated populations to the north on the Mexican Plateau and to the southeast in the highlands of Oaxaca. The populations on the Mexican Plateau were subjected to considerable climatic fluctuations in the Pleistocene. At glacial or pluvial times the frogs dispersed over the plateaus and extended northward into Arizona and New Mexico, whereas during interglacial times their ranges were constricted to higher, more mesic areas. A variety of minor morphological, color, and ethological differentiation took place in the populations, which were alternatively isolated and confluent. The result of this history is the mosaic of varieties of *Hyla eximia*.

The southeastern Mexican populations of the *eximia* group differentiated from the northern populations, and dispersed through the elevated region of Oaxaca and across the Isthmus of Tehuantepec into the Chiapan highlands. The dispersal across the isthmus must have occurred in late Pliocene or during an early Pleistocene glacial period. Subsequent differentiation on either side of the isthmus resulted in the evolution of *euphorbiacea* in the Oaxacan highlands and *walkeri* in the Chiapan-Guatemalan highlands.

*Hyla cadaverina* apparently is an early divergent line from the *eximia-regilla* stock and became adapted for existence in sub-humid areas with the onset of increasing

aridity in the Pliocene, whereas the *regilla* stock remained in more mesic montane environments. The dispersal of *regilla* southward into southern Baja California probably occurred in a Pleistocene pluvial period. Subsequent isolation resulted in minor differentiation of the southern population into *Hyla regilla curta*.

#### THE WEST INDIAN HYLIDS

There is no evidence that any Middle American hylids were derived from the depauperate West Indian hylid fauna, but it is possible that some of the West Indian hylids were derived from Middle America. Dunn (1926) considered the four Jamaican species to have resulted from a single invasion of that island from Hispaniola, which also contains four species. The only other true West Indian hylid is *Hyla septentrionalis* on Cuba, Isle of Pines, the Bahamas, and southern peninsular Florida. Discounting the continental islands of Trinidad and Tobago, the only other *Hyla* on a West Indian Island is the South American *Hyla rubra* on St. Lucia. Thus, we can view the West Indian hylid fauna as being comprised of nine endemic species—four on Hispaniola, four on Jamaica, and one centered on Cuba and the Bahamas.

On evidence provided by a study of the cranial osteology, Trueb (1970a) concluded that a *Hyla septentrionalis* group containing *septentrionalis*, *domineensis*, *vasta*, *brunnea*, and *lichenata* possibly evolved from a *Hyla boans*-like progenitor that waited to the West Indies from South America. She considered that two phyletic lines are evident in the group. One of these contains as the primitive form *Hyla vasta* on Hispaniola; *domineensis* on Hispaniola and *septentrionalis* on Cuba are treated as derived species. Trueb placed the Jamaican *Hyla brunnea* and *lichenata* in a second phyletic line in the *septentrionalis* group and concluded that they probably originated *in situ* from a common ancestor that migrated from Hispaniola.

Dunn's (1926) supposition that all of the Hispaniolan hylids are closely related can be disproved. Certainly *Hyla heilprini* with its green peritoneum, external pigmentation, and projecting prepollex is strongly suggestive of a South American *Hyla albomarginata* group

progenitor, despite Noble's (1927) contention that *heilprini* is a montane derivative of *vasta*. The relationships of the small *Hyla pulchri-lineata* are not known. Certainly it represents a separate stock from *heilprini* and the *septentrionalis* group.

The two small Jamaican species, *Hyla marianae* and *wilderi*, were placed by Dunn (1926) with the larger species on the island—*brunnea* and *lichenata*. The bromeliad breeding behavior and similar adaptive types of tadpoles in all four species were his principal criteria for placing all of the species in one group. Dunn concluded that the speciation in the Jamaican hylids was the result of "fratricidal competition" in the tadpoles, which resulted in the metamorphosis of frogs at greatly varying sizes. Granting that Dunn's conclusions represent one solution to the problem of the Jamaican hylids, I question the validity of his argument and suggest that new evidence be sought. Trueb's suggested relationships of the Jamaican *Hyla brunnea* and *lichenata* with the *septentrionalis* group are based on the supposition that the ancestral stock that reached Jamaica was a casque-headed form. The development of a casque

head is specialized. Casque-headed hylids are considered to be at the ends of various phyletic lines and not to be ancestors of more generalized forms. However, Dunn's theory of the pedomorphic status of *wilderi* and *marianae* offers an intriguing possibility that might be substantiated by developmental studies of the Jamaican species.

Although *Hyla wilderi* and *marianae* have highly specialized arboreal tadpoles, it is conceivable that they evolved the larval characteristics independently of *brunnea* and *lichenata*. I find no apparent close relationship of *wilderi* and *marianae* with Hispaniolan species and suggest the possibility that these two species might be derivatives of a generalized Mesoamerican hylid stock. The two Jamaican species do not possess any morphological characters that rule out this possibility.

The foregoing comments on West Indian hylids are not intended to be conclusive but rather, I hope, inductive to stimulate research on this group of hylids. Except for Trueb's (1970a) comments on the cranial osteology of some of the species, no new information has come forth after Dunn's (1926) work on the Jamaican species.

## SUMMARY AND CONCLUSIONS

One hundred and fifteen species of hylid frogs are known from Middle America (México and Central America). On the bases of morphological characters of the adults and tadpoles, and features of their life histories, these species are placed in 15 genera. Six of these genera are endemic to Middle America, and two others have their greatest diversity in Middle America. The 73 species of *Hyla* in Middle America are arranged into 28 groups, 18 of which are restricted to Middle America.

The following taxonomic changes are proposed in this paper: 1) *Hyla arboricola* Taylor, 1941=*Hyla eximia* Baird, 1854. 2) *Hyla bocourti* Mocquard, 1899=*Hyla euphorbiacea* Günther, 1859. 3) *Hyla cardenasi* Taylor, 1939=*Hyla eximia* Baird, 1854. 4) *Hyla darlingi* Smith, Smith, and Werler, 1952=*Hyla miotympanum* Cope, 1863. 5) *Hyla regilla deserticola* Jameson, Mackey, and Richmond, 1966=*Hyla regilla hypochondriaca* Hallowell, 1854. 6) *Hyla duellmani* Lynch and Smith, 1966=*Hyla chaneque* Duellman, 1961. 7) *Hyla immensa* Taylor, 1952=*Hyla miliaria* (Cope, 1886). 8) *Hyla lythrodes* Savage, 1968=*Hyla rufoculis* Taylor, 1952. 9) *Hyla phantasmargoria* Dunn, 1943=*Hyla miliaria* (Cope, 1886). 10) *Hyla pugnax* Schmidt, 1857=*Hyla crepitans* Wied, 1824. 11) *Hyla richardtaylori* Taylor, 1954=*Hyla fimbrimembra* Taylor, 1948. 12) *Hyla wrightorum* Taylor, 1939=*Hyla eximia* Baird, 1854. 13) *Cerathyla Jiménez de la Espada*, 1871=*Hemiphractus* Wagler, 1828. No new taxa are proposed.

The present study represents the first attempt to work out the systematics of a large, diverse group of frogs by utilizing characters such as cranial osteology, mating calls, and larval morphology, in addition to the conventional external morphological characters of the adults. The utilization of a wide spectrum of characters has provided a wealth of evidence concerning the relationships of the species.

A variety of modes of life history is exhibited by the Middle American hylids. The evolution of stream adaptations in tadpoles apparently has occurred at least twice in Middle America. Probably the habit of depositing eggs in bromeliads has evolved independently in three groups.

Although there is considerable continuity in the hylid fauna of the lowlands, the relatively depauperate fauna on the Pacific lowlands is distinct from that on the Caribbean lowlands. Significant faunal breaks occur at the Isthmus of Tehuantepec and the Nicaraguan Depression. The hylids in the three major highland areas are quite distinct; the highest percentage of endemism occurs in the highlands of Costa Rica and Western Panamá. No species is shared between these highlands and those in Nuclear Central America, which has five species in common with the Mexican highlands.

The hylid fauna of Middle America contains three historical elements. The major element is the Mesoamerican fauna, which evolved in tropical Middle America from early South American stocks that were isolated in Middle America during most of the Cenozoic. A significant part of the present Middle American hylid fauna is composed of species belonging to the Neotropical fauna. These are late Cenozoic immigrants into Central America. A third, relatively insignificant group is the Nearctic fauna, a part of the Holarctic hylid fauna that reaches its southern limits of distribution in the New World in northern Middle America.

The lengthy presentation of my researches on Middle American hylid frogs answers many questions and raises several others. The relationships of some species are unknown. Although I have been tempted to invoke the doctrine of special creation, I have followed the precedent established by Lucretius (58 B.C.): "Nothing from nothing ever yet was born."



## APPENDIX 1

All of the specimens of hylids from Middle America that have been examined during the course of this study are listed below. The species are arranged alphabetically within the genera, which in turn are in alphabetical order. Localities and specimens are given in the following order: country (arranged from north to south—México, British Honduras, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panamá); states (departments, provinces) in alphabetical order in each country; localities in alphabetical order in each state; museum abbreviations are given in alphabetical order as listed in Materials and Methods, and the number of specimens in each museum collection are given in parentheses. Unless otherwise indicated, specimens are preserved frogs. Skeletons, lots of tadpoles, and clutches of eggs are so indicated. No distinction is made between cleared and stained specimens and those that are dried skeletons. For example, K.U. (16, 2 skeletons, 1 tadpoles) denotes that from a given locality there are in the collections at the University of Kansas, 16 preserved frogs, two skeletons, and one lot of tadpoles. Localities that have not been located to state or equivalent political unit are listed immediately after the name of the country. Specimens with data giving only the country or state are listed first in that political unit under "No specific locality."

### *Acris crepitans blanchardi*

MEXICO: *Coahuila*: 19 kilometers north of Jiménez, 19 kilometers west of Jiménez, K.U. (10); 1.6 kilometers west of Jiménez, K.U. (1); 3.2 kilometers west of Jiménez, K.U. (10); Río Sabinas, near Múzquiz, F.M.N.H. (11).

### *Agalychnis annae*

COSTA RICA: *Alajuela*: Cinchona, K.U. (2 tadpoles). *Cartago*: Cartago, A.N.S.P. (4), F.M.N.H. (13), K.U. (73, 1 skeleton); Moravia, K.U. (4, 1 tadpoles, 1 eggs), U.S.C. (1); 2 kilometers south of Paraiso, U.S.C. (3); Tapantí, K.U. (39, 5 skeletons, 10 tadpoles, 4 eggs), M.C.Z. (2), M.V.Z. (3), U.I.M.N.H. (1), U.S.C. (1). *Guanacaste*: El Silencio, La Laguna, U.S.C. (3). *Limón*: Jiménez, A.M.N.H. (1). *San José*: Guadalupe, K.U. (1); U.S.C. (1); La Hondura, A.N.S.P. (1); La Palma, K.U. (1, 7 tadpoles, 2 eggs), M.C.Z. (1), U.S.C.

(1); San José, A.M.N.H. (3), A.N.S.P. (16), K.U. (2), M.C.Z. (2), S.U. (1), U.M.M.Z. (9), U.S.C. (12); San Pedro, A.M.N.H. (3), U.S.C. (12); Santo Domingo, M.V.Z. (4).

### *Agalychnis calcarifer*

COSTA RICA: *Heredia*: Finca La Selva, U.S.C. (1). *Limón*: Siquirres, N.H.R.M. (1).

PANAMA: *Canal Zone*: Barro Colorado Island, A.N.S.P. (1), F.M.N.H. (1), M.C.Z. (1). *Darién*: Laguna, K.U. (3, 1 eggs).

### *Agalychnis callidryas*

MEXICO: *Campeche*: 7.5 kilometers west of Escárcega, K.U. (5); Matamoros, F.M.N.H. (1); Pacaitún, F.M.N.H. (1); Tuxpeña, U.M.M.Z. (1). *Oaxaca*: 3 kilometers north of Donají, U.M.M.Z. (10); 22 kilometers south of Jesús Carranza (Veracruz), U.I.M.N.H. (6); 3.7 kilometers north of Sarabia, U.M.M.Z. (8); 3 kilometers south of Tolocita, K.U. (6); Tuxtepec, K.U. (1, 1 tadpoles); 1 kilometer south of Uvero, U.M.M.Z. (27); 1 kilometer north of Valle Nacional, U.I.M.N.H. (10); 1.6 kilometers south of Valle Nacional, K.U. (23, 4 skeletons, 1 tadpoles), U.I.M.N.H. (18). *Tabasco*: 10 kilometers south of Cárdenas, K.U. (1); La Venta, U.S.N.M. (2); Santo Tomás, U.S.N.M. (1); Teapa, U.M.M.Z. (9, 2 tadpoles); 10 kilometers north of Teapa, U.M.M.Z. (2); 13 kilometers north of Teapa, U.M.M.Z. (2); 21 kilometers north of Teapa, U.M.M.Z. (1). *Veracruz*: 7 kilometers south of Acayucan, U.I.M.N.H. (1); 33 kilometers south of Acayucan, U.I.M.N.H. (2); 1.6 kilometers east southeast of Alvarado, U.M.M.Z. (5); 2.4 kilometers east-southeast of Alvarado, U.M.M.Z. (2); 4.5 kilometers south of Aquilera, U.M.M.Z. (1); Berta, U.S.N.M. (1); 10 kilometers south of Catemaco, U.M.M.Z. (1); 8 kilometers southwest of Coatzacoalos, U.M.M.Z. (9); Cuatutolapam, U.M.M.Z. (33); Encinal, U.M.M.Z. (20); 10 kilometers southeast Hueyapan, U.M.M.Z. (5); 21.6 kilometers south of Las Choapas, T.C.W.C. (1); 24.8 kilometers south of Las Choapas, T.C.W.C. (2); 3.5 kilometers west of Lerdo de Tejada, U.M.M.Z. (4); 2 kilometers south of Naranja, K.U. (1 skeleton), U.M.M.Z. (17); Rodríguez Clara, U.I.M.N.H. (1); San Andrés Tuxtla, U.I.M.N.H. (6); 2 kilometers south of San Andrés Tuxtla, U.M.M.Z. (2); Tierra Colorada, C.A.S. (1), S.U. (2), U.I.M.N.H. (12); 8 kilometers south of Veracruz, U.M.M.Z. (4); 8 kilometers south of Veracruz, U.M.M.Z. (4); 8 kilometers east of Zapopan, T.O.W.C. (1). *Yucatán*: Chichén-Itzá, F.M.N.H. (29), U.M.M.Z. (1) 2.4 kilometers east of Chichén-Itzá, U.M.M.Z. (1 tadpoles); 10 kilometers south of Chichén-Itzá, U.M.M.Z. (4, 1 tadpoles); Culuba, 28 kilometers east of Sucopo, F.M.N.H. (13).

BRITISH HONDURAS: *Cayo*: Colhune Ridge, U.M.M.Z. (6); Pine Ridge Road, U.M.M.Z. (4).

GUATEMALA: *Alta Verapaz*: Finca Chamá, U.M.M.Z. (66, 1 eggs); Finca Samanzana, U.M.M.Z. (2 tadpoles). *El Petén*: 3 kilometers southeast of La Libertad, K.U. (7); Tikal, U.M.M.Z. (8); Sacrificio, A.M.N.H. (1); Toocog, 15 kilometers southeast of La Libertad, K.U. (13, 12 skeletons, 1 tadpoles, 2 eggs). *Izabal*: 8 kilometers south of Puerto Barrios, K.U. (8).

HONDURAS: *Atlantida*: Lancetilla, M.C.Z. (1); Toloa Junction, U.S.N.M. (1). *Colón*: Balfate, A.M.N.H. (2). *Cortés*: Agua Azul, A.M.N.H. (4); Lago Yojoa, A.M.N.H. (6); Río Lindo, A.M.N.H. (2).

NICARAGUA: *Boaco*: 14 kilometers north of, 13 kilometers east of Boaco, K.U. (1). *Jinotega*: Jinotega, F.M.N.H. (1). *Managua*: Casa Colorada, 22 kilometers south of Managua, K.U. (5, 1 skeleton, 2 tadpoles, 3 eggs). *Matagalpa*: Finca Tepeyac, K.U. (9, 1 tadpoles); Hacienda La Cumplida, K.U. (2, 1 skeleton, 1 eggs), U.M.M.Z. (18, 3 tadpoles). *Zelaya*: Bluefields, F.M.N.H. (1); Cukra, A.M.N.H. (1); El Recreo, K.U. (1); Isla Pequeña del Maíz, M.C.Z. (2); Masahuas, Río Huaspuc, A.M.N.H. (1); Río Grande, M.C.Z. (1).

COSTA RICA: *Alajuela*: Laguna Monte Alegre, K.U. (1); 3 kilometers northeast of Muelle de Arenal, U.S.C. (2). *Cartago*: Peralta, K.U. (1); Turrialba, K.U. (8), U.M.M.Z. (5), U.S.C. (10). *Guanacaste*: Finca San Bosco, K.U. (65, 5 skeletons, 1 tadpoles, 3 eggs), U.S.C. (35); Silencio, U.S.C. (16); Tilarán, K.U. (2). *Heredia*: Finca La Selva, U.M.M.Z. (1); Puerto Viejo, K.U. (2). *Limón*: Batán, K.U. (2); Colorado Bar, A.M.N.H. (1); El Tigre, 9 kilometers southwest of Siquirres, U.S.C. (1). Cuápiles, A.N.S.P. (1); La Castilla, A.N.S.P. (3); La Lola, U.F. (1), U.S.C. (4); 1.6 kilometers south of Limón, A.M.N.H. (1); Los Diamantes, U.M.M.Z. (2); Pandora, U.S.C. (7); Río Lari at Río Dipnari, U.S.C. (2); Río Toro Amarillo, 7 kilometers west of Cuápiles, K.U. (1 tadpoles); Suretka, K.U. (3); Tortugero, M.C.Z. (2), U.F. (3). *Puntarenas*: 3 kilometers northwest of Buenos Aires, K.U. (1); 6 kilometers northwest of Buenos Aires, K.U. (2); 10 kilometers east of Esparta, K.U. (1, 1 tadpoles); Colfío, U.M.M.Z. (3), U.S.C. (8); 4 kilometers east southeast of Palmar Sur, K.U. (1); Parrita, U.S.C. (9), 10 kilometers northwest of Piedras Blancas, K.U. (4); 8 kilometers northeast of Potrero Grande, U.S.C. (1); 4.5 kilometers west of Rincón de Osa, K.U. (2, 1 tadpoles); Río Ferruviosa, 7.2 kilometers south of Rincón de Osa, U.S.C. (1); 21.7 kilometers west of San Ramón, U.S.C. (14); 1.6 kilometers northwest of Villa Neily, U.S.C. (3). *San José*: San Isidro el General, K.U. (4); 14 kilometers southwest of San Isidro el General, U.S.C. (1); 19 kilometers southwest of San Isidro el General, K.U. (2).

PANAMA: *Boas del Toro*: 3.2 kilometers northwest of Almirante, K.U. (5); 9.6 kilometers west of Almirante, K.U. (1); 12.8 kilometers west of Almirante, K.U. (1); Cayo de Agua, K.U. (3); Cayo Zapatilla Grande, K.U. (5); Isla de Colón, K.U. (4); Isla Popa, K.U. (1); mouth of Río Cahuita, K.U. (1). *Canal Zone*: Barro Colorado Island, A.M.N.H. (3), A.N.S.P. (1), F.M.N.H. (2) K.U. (5, 4 skeletons, 5

tadpoles, 2 eggs), T.N.H.C. (2); U.M.M.Z. (1); Camp Chagras, K.U. (4, 1 tadpoles); Gatún, C.A.S. (1), M.C.Z. (1); Juan Mina, A.N.S.P. (2); Madden Forest, A.M.N.H. (7); 3.5 kilometers north of Miraflores bridge, T.N.H.C. (19); San Pablo, M.C.Z. (1). *Chiriquí*: 13 kilometers west-northwest of Concepción, K.U. (1); Progreso, U.M.M.Z. (1); Puerto Armuelles, C.A.S. (1). *Colón*: Achioté, K.U. (4). *Darién*: Camp Creek, below Yavisa, A.M.N.H. (1); Chalichiman's Creek, Río Sucubtí, A.M.N.H. (2); Laguna, K.U. (13, 3 tadpoles); Río Chucunaque at Río Cancón, U.M.M.Z. (1); Río Tuira at Río Mono, K.U. (18); Río Ucurgantí, 7 kilometers above mouth, K.U. (3); Tacarcuna, K.U. (19, 2 skeletons, 2 tadpoles, 2 eggs). *Panamá*: Cerro La Campana, F.M.N.H. (25), K.U. (33, 2 tadpoles, 7 eggs), U.U. (4); 3 kilometers west-southwest of Chepo, K.U. (1); Tapia, A.M.N.H. (2).

#### *Agalychnis litodryas*

PANAMA: *Darién*: Río Tuira at Río Mono, K.U. (1).

#### *Agalychnis moreletii*

MEXICO: *Chiapas*: Acacoyagua, U.M.M.Z. (1 eggs); 6 kilometers northeast of Escuintla, U.M.M.Z. (6, 1 tadpoles); Finca San Jerónimo, U.M.N.H. (14); Finca Juárez, S.U. (2), U.I.M.N.H. (22), U.M.M.Z. (4), Región Soconusco, U.I.M.N.H., U.I. (3). *Oaxaca*: Campamento Vista Hermosa, K.U. (2, 1 tadpoles); Mirador, A.M.N.H. (10); Nuevo Raza Sacatepec, U.I.M.N.H. (1); 28.2 kilometers north of Pochutla, U.M.M.Z. (1). *Veracruz*: Cuautlapan, K.U. (3), U.I.M.N.H. (6), U.M.M.Z. (1), U.S.N.M. (11); Escamilla, U.M.N.H. (5); 6.4 kilometers east of Fortín de las Flores, C.A.S. (1); 8 kilometers east of Orizaba, C.A.S. (1); San Andrés Tuxtla, U.S.N.M. (1); Volcán San Martín, K.U. (1).

BRITISH HONDURAS: No specific locality, F.M.N.H. (2). *Cayo*: Pine Ridge Road, U.M.M.Z. (22); Valentin, U.M.M.Z. (14).

GUATEMALA: No specific locality. U.S.N.M. (5). *Alta Verapaz*: Finca Chichén, U.M.M.Z. (5); Finca Chicoyou, K.U. (66, 2 skeletons, 5 tadpoles, 4 eggs); Finca La Primavera, U.M.M.Z. (1); Finca Samac, U.M.M.Z. (3, 1 tadpoles); Finca Volcán, U.M.M.Z. (3); Senahú, U.S.N.M. (1). *Huehuetenango*: Barillas, U.M.M.Z. (4); Finca San Rafael, 16 kilometers southeast of Barillas, F.M.N.H. (4); Maxhal, north of Barillas, F.M.N.H. (1). *Santa Rosa*: Finca El Progreso, U.M.M.Z. (9); Finca La Cloria, U.M.M.Z. (2); *Suchitepequez*, Patutul, F.M.N.H. (1).

#### *Agalychnis saltator*

NICARAGUA: *Zelaya*: Eden Mine, A.N.S.P. (2).

COSTA RICA: *Guanacaste*: Finca San Bosco, K.U. (27, 1 skeleton), S.U. (2), U.S.C. (1). *Heredia*: Finca La Selva, U.S.C. (1); Puerto Viejo, K.U. (15, 2 skeletons, 1 tadpoles). *Limón*: La Castilla, A.N.S.P. (1).

*Agalychnis spurrelli*

COSTA RICA: *Puntarcnas*: Rincón de Osa, K.U. (1), U.S.C. (1); 4.5 kilometers west of Rincón de Osa, U.S.C. (1), K.U. (3 tadpoles, 1 eggs); Río Ferroviosa, 7 kilometers south of Rincón de Osa, U.S.C. (4). *San José*: 16 kilometers southwest of San Isidro el General, U.S.C. (12).

PANAMA: *Bocas del Toro*: Río Urri, R.H. (1). *Canal Zone*: Barro Colorado Island, A.M.N.H. (1), A.N.S.P. (1), M.C.Z. (1), K.U. (8, 1 skeleton, 1 tadpoles). *Darién*: Tacarcuna, K.U. (9). *Panamá*: Cabima, U.S.N.M. (1).

*Anotheca spinosa*

MEXICO: *Oaxaca*: Vista Hermosa, K.U. (13, 4 skeletons, 2 tadpoles), U.M.M.Z. (2); Yelagago, A.M.N.H. (1); 8 kilometers south of Yetla, K.U. (1). *Veracruz*: Barranca Metlac, U.M.M.Z. (1); Cuautlapán, F.M.N.H. (48), K.U. (3), M.C.Z. (11), U.I.M.N.H. (62), U.M.M.Z. (18, 1 skeleton), U.S.N.M. (14); 9 kilometers southwest of Fortín de las Flores, U.M.Z. (9); 13 kilometers west northwest of Potrero, K.U. (2); Volcán San Martín, K.U. (3, 1 tadpoles), U.M.M.Z. (5, 1 tadpoles).

COSTA RICA: *Alajuela*: 3 kilometers west of La Fortuna, U.S.C. (1). *Cartago*: Moravia, K.U. (2); Paloma, Valle de Orosi, U.S.N.M. (1).

PANAMA: *Bocas del Toro*: Río Changena, 830 meters, K.U. (2). *Cocle*: El Valle, U.M.M.Z. (1).

*Gastrotheca ceratophrys*

PANAMA: *Bocas del Toro*: 5 kilometers west of Almirante, K.U. (1); Río Changena, 830 meters, K.U. (1); Río Claro near junction with Río Changena, K.U. (3, 1 skeleton). *Darién*: Laguna, K.U. (1); Tacarcuna, U.S.N.M. (1). *Panamá*: Upper Río Pequeni, U.S.N.M. (1). *San Blas*: Camp Summit (3).

*Gastrotheca nicefori*

PANAMA: *Darién*: South slope of Cerro Citurio, Serranía de Pirre, K.U. (2); Ridge between Río Jaque and Río Inamado, Serranía del Sapo, K.U. (1).

*Hemiphractus panamensis*

PANAMA: *Bocas del Toro*: north slope Cerro Pando, 1450 meters, K.U. (1); Río Changena, B.Y.U. (1 + young), R.H. (1). *Colón*: Signal Loma, 5 kilometers south of Santa Isabel, U.S.N.M. (2). *Darién*: Cerro Citurio, K.U. (18), Cerro Pirre, G.M.L. (1), K.U. (5, 2 skeletons). *Panamá*: Altos de Pacora, K.U. (2). *San Blas*: Camp Summit, K.U. (3).

*Hyla altipotens*

MEXICO: *Oaxaca*: 33 kilometers north of San Gabriel Mixtepec, K.U. (1); 37 kilometers north of San Gabriel Mixtepec, K.U. (25, 2 skeletons); 3 kilometers east of San Sebastian (Los Fustes), T.C.W.C. (1).

*Hyla angustilincata*

COSTA RICA: *Heredia*: Rama Sur Río Las Vueltas, south slope of Volcán Barba, K.U. (21, 2 skeletons, 4 tadpoles), M.C.Z. (2), U.S.C. (2). *Puntarcnas*: 3 kilometers east-northeast of Monteverde, U.S.C. (2). *San José*: La Palma, U.S.N.M. (3).

*Hyla arboreascendens*

MEXICO: *Hidalgo*: 10 kilometers south of Zacualtipán, I.P.N. (2). *Oaxaca*: 4.2 kilometers south of Campamento Vista Hermosa, K.U. (14, 1 skeleton, 1 tadpoles); 6 kilometers south of Campamento Vista Hermosa, K.U. (9, 1 skeleton); 7.5 kilometers south of Campamento Vista Hermosa, K.U. (1); 10 kilometers south of Campamento Vista Hermosa, K.U. (4); 15 kilometers south of Campamento Vista Hermosa, K.U. (2), U.M.M.Z. (1); Cerro Machín, U.I.M.N.H. (3); Cerro San Felipe, F.M.N.H. (3), U.I.M.N.H. (4), U.S.N.M. (1); 13 kilometers northwest of Ixtlán de Juárez, T.N.H.C. (3); 25.5 kilometers north of Nochistlán, U.I.M.N.H. (2); 52 kilometers north of Oaxaca, U.I.M.N.H. (2). 68 kilometers south of Valle Nacional, U.M.M.Z. (4). *Puebla*: 14.4 kilometers west of Huachinango, Parajé Verde, U.I.M.N.H. (2), U.S.N.M. (7); Puente Colorado, U.I.M.N.H. (2), U.M.M.Z. (1); Río Octapa, 3.7 kilometers north-northeast of Tezuitlán, K.U. (9, 1 skeleton). *Tlaxcala*: Apizaco, U.S.N.M. (1). *Veracruz*: Acultzingo, F.M.N.H. (2) I.P.N. (1), U.I.M.N.H. (4); 5 kilometers southwest of Acultzingo, U.I.M.N.H. (1); Cumbres de Acultzingo, F.M.N.H. (3), U.I.M.N.H. (5), U.M.M.Z. (16), U.S.N.M. (5). 1.9 kilometers southwest of La Joya, F.M.N.H. (30); La Perla, M.C.Z. (1); Pan de Olla, M.C.Z. (2), U.I.M.N.H. (17); U.S.N.M. (25); Tegueyutepec, M.C.Z. (3).

*Hyla arenicolor*

MEXICO: *Aguascalientes*: 29 kilometers west, 3 kilometers south of Aguascalientes, K.U. (1); 14.4 kilometers north of Rincón de Romos, U.I.M.N.H. (1). *Chihuahua*: Balleza, U.S.N.M. (1); north rim of Barranca del Cobre, 37 kilometers south, 2.4 kilometers east of Creel, K.U. (8); Batopilas, U.S.N.M. (1); Chihuahua, U.M.M.Z. (1); 24 kilometers south, 10 kilometers east of Creel, K.U. (3); Divisadero, 25.6 kilometers south, 21 kilometers west of Creel, K.U. (13); 21 kilometers west of Guatemoc, M.C.Z. (1); 13 kilometers southwest of Hidalgo del Parral, T.C.W.C. (1); 60 kilometers southwest of Juanito, U.S.N.M. (1); La Pulvosa, U.M.M.Z. (2); Maguarichic, U.M.M.Z. (2); 3 kilometers west of Minaca, K.U. (2); Mojarachic, F.M.N.H. (2), U.I.M.N.H. (1), U.M.M.Z. (1); Río del Sauz, west of Sauz, A.M.N.H. (1); 3 kilometers south, 8 kilometers west of San Francisco, K.U. (3); San Rafael, between Santa Barbara and Parral, A.M.N.H. (1); Sauz, F.M.N.H. (1); 5 kilometers northeast of Temoris, K.U. (8); Wasichichic, U.M.M.Z. (1). *Coahuila*: No specific locality, F.M.N.H. (3). *Distrito Federal*: Pedregal de San Angel, I.P.N. (1); 2.5 kilometers west of



- Santa Fe, A.M.N.H. (1). *Durango*: No specific locality, U.S.N.M. (1); Cerro de Mercado, A.N.S.P. (1); Coyotes, U.M.M.Z. (1); El Salto, U.S.N.M. (1); 42.7 kilometers northeast of El Salto, U.I.M.N.H. (6); 1.6 kilometers west of El Salto, L.B.S.C. (2); 5 kilometers west of El Espinosa, L.B.S.C. (1); Laguna del Progreso, U.M.M.Z. (3); 50 kilometers southwest of Victoria de Durango, U.I.M.N.H. (2). *Guanajuato*: No specific locality, U.S.N.M. (4); 6 kilometers west of Acámbaro, F.M.N.H. (1); 6 kilometers north of, 8 kilometers west of León, K.U. (1); 11 kilometers northwest of León, U.I.M.N.H. (5); 7 kilometers south of Valle de Santiago, U.I.M.N.H. (1). *Guerrero*: No specific locality, U.M.M.Z. (1); Acahuitzotla, K.U. (1), T.C.W.C. (9); 3 kilometers north of Acahuitzotla, F.M.N.H. (5), U.I.M.N.H. (1); Agua del Obispo, F.M.N.H. (4), T.C.W.C. (1), U.I.M.N.H. (3), U.M.M.Z. (1). Chilapa, U.S.N.M. (1); east of Chilapa, K.U. (1); 5 kilometers south of Chilpancingo, U.F. (2); 19 kilometers south of Chilpancingo, F.M.N.H. (22), U.I.M.N.H. (15); Palo Blanco, F.M.N.H. (1), U.I.M.N.H. (1); 18 kilometers south of Puente de Ixtla (Morelos), F.M.N.H. (4), U.I.M.N.H. (8); San Juan, U.S.N.M. (1); 8 kilometers north of Taxco, T.C.W.C. (2). *Hidalgo*: 18 kilometers southeast of Actopan, K.U. (2), T.C.W.C. (13); 8 kilometers west of Actopan, T.C.W.C. (4); 30 kilometers east of Huichapan, T.C.W.C. (5); 11 kilometers southwest of Huichapan, K.U. (1); 9.4 kilometers north of Metzquitlán, K.U. (1); Miguel, M.C.Z. (1); Tianguistengo, F.M.N.H. (1). *Jalisco*: No specific locality, U.S.N.M. (2); 11 kilometers west of Ameca, U.M.M.Z. (2); Atemaje, A.M.N.H. (2); 3 kilometers west of Ayutla, K.U. (5), Cerro del Col, A.M.N.H. (1); Cerro Pelón, Río Blanca, north of Zapopan, A.M.N.H. (2); Chapala, U.S.N.M. (1); 4 kilometers northeast of Ciudad Guzmán, F.M.N.H. (1); 8 kilometers northwest of Cuautla, K.U. (1); 5 kilometers northwest of Degollado, K.U. (1); Guadalajara, K.U. (10); 5 kilometers north of Guadalajara, K.U. (2); 33 kilometers southwest of Cuadalajara, K.U. (2); Hostolipaquillo, A.M.N.H. (4); 3 kilometers east of Ixtlahuacán del Río, A.M.N.H. (1); 10.4 kilometers north-northwest of Ixtlahuacán del Río, K.U. (1); La Mesa María de León, K.U. (11); 5 kilometers northeast of Magdalena, K.U. (4); Rancho Primavera, near Cuadalajara, U.I.M.N.H. (2); Río Blanco, near Cuadalajara, K.U. (2); San Gabriel, U.M.M.Z. (1); 3 kilometers northeast of Talpa, K.U. (2); 7 kilometers west of Tenchitlán, K.U. (1); between Tequesquite and Hostolipaquillo, A.M.N.H. (5); Tlaquepaque, A.M.N.H. (7); Tonolá, A.M.N.H. (2); between Tonolá and Tlaquepaque, A.M.N.H. (1); 14.4 kilometers northeast of Unión Tula, K.U. (1); 2.5 east of Villa Cuerrero, K.U. (1); 6.4 kilometers west of Villa Cuerrero, K.U. (5); 1.2 kilometers north of, 11 kilometers west of Yahualica, K.U. Yahualica, K.U. (2). *México*: 11 kilometers south of Yahualica, K.U. (2). *México*: 11 kilometers south of, Acambay, K.U. (1); San Juan Teotihuacán, K.U. (1), M.C.Z. (2), U.M.M.Z. (1); Tonicato, I.P.N. (1). *Michoacán*: Agua Cerca, U.M.M.Z. (1); Cascada Tzararacua, U.M.M.Z. (5); Chinapa, U.M.M.Z. (1); 6 kilometers east of Cojumatlán, F.M.N.H. (1), U.I.M.N.H. (1); Dos Aguas, U.M.M.Z. (1); El Espinal, U.M.M.Z. (1); El Sabino, F.M.N.H. (22), U.I.M.N.H. (6); Lago de Camécuaro, U.M.M.Z. (1); Lombardia, U.M.M.Z. (2); Tupátaro, U.S.N.M. (1); 1.2 kilometers northwest of Zinapécuaro, K.U. (1). *Morelos*: 19 kilometers north of Cuautla, T.C.W.C. (2); 18 kilometers southeast of Cuautla, T.N.H.C. (4); Cuernavaca, U.I.M.N.H. (3), U.M.M.Z. (2), U.S.N.M. (1); 3 kilometers north of Cuernavaca, F.M.N.H. (4); 11 kilometers east of Cuernavaca, U.I.M.N.H. (2); Huajintlán, F.M.N.H. (6); 2 kilometers south of Jonacatepec, T.C.W.C. (3). *Nayarit*: 1.6 kilometers east of Ixtlán del Río, U.M.M.Z. (1); La Mesa de Nayarit, A.M.N.H. (4); Sierra de Nayar, A.M.N.H. (1); 37 kilometers south of Tepic, L.B.S.C. (6). *Oaxaca*: 3 kilometers east of Huajapan de León, K.U. (1); 32 kilometers southeast of Huajapan de León, U.I.M.N.H. (1). *Puebla*: 13 kilometers southeast of Izúcar de Matamoros, C.A.S. (1). *Querétaro*: Cadercyta, U.M.M.Z. (3); 11 kilometers west-southwest of San Juan del Río, K.U. (1); Tequisquiapan, A.M.N.H. (3). *San Luis Potosí*: Ahualulco, U.S.N.M. (1); Alvarez, M.C.Z. (2), Cerro de Alvarez, A.N.S.P. (2); Cerro de Miguclito, A.N.S.P. (3); Morales, M.C.Z. (1); U.M.M.Z. (1); San Luis Potosí, M.C.Z. (5), U.I.M.N.H. (4); 36 kilometers north of San Luis Potosí, M.C.Z. (4); 43 kilometers south of San Luis Potosí, M.C.Z. (6); 18 kilometers southwest of San Luis Potosí, U.M.M.Z. (3); 5 kilometers west of San Luis Potosí, U.I.M.N.H. (8); San Pedro, A.N.S.P. (1); 3 kilometers north of Santa María del Río, A.M.N.H. (1). *Sinaloa*: No specific locality, U.S.N.M. (2); Plumas, U.S.N.M. (1); 70 kilometers northeast of Villa Unión, L.B.S.C. (6), 75 kilometers northeast of Villa Unión, L.B.S.C. (1). *Sonora*: 14.4 kilometers north of Imuris, K.U. (1); 3 kilometers from La Poza, 10 kilometers north of Cuaymas, F.M.N.H. (6); Nogales, U.S.N.M. (1); Pilares, U.M.M.Z. (5); San José de Guayamas, M.C.Z. (1); northern Sonora, U.S.N.M. (1). *Veracruz*: 10 kilometers southwest of Jcales, K.U. (2); 6 kilometers west-southwest of Zacualpilla, K.U. (73). *Zacatecas*: 3 kilometers southeast of Laguna Valderana, U.M.M.Z. (3); 17.6 kilometers northwest of Jalpa, K.U. (3); 13 kilometers south of Moyahua, C.A.S. (1); Plateado, U.S.N.M. (1); 5 kilometers northwest of Teul, U.M.M.Z. (40).

#### *Hyla bistincta*

MEXICO: *Durango*: 5 kilometers west of El Espinosa, L.B.S.C. (1). *Guerrero*: Omiltemi, U.I.M.N.H. (3); between Puerto Chico and Asoladero, U.M.M.Z. (1); 22 kilometers southwest of Yextla, I.P.N. (8). *Hidalgo*: Zacualtipán, A.N.S.P. (1). *Jalisco*: 25 kilometers southeast of Autlán, U.M.M.Z. (1). *México*: 19 kilometers west of Villa Victoria, U.I.M.N.H. (1). U.S.N.M. (1). *Morelos*: Cuernavaca, U.S.N.M. (1); 3 kilometers north of Cuernavaca, U.I.M.N.H. (3). *Michoacán*: Cerro San Andrés, U.M.M.Z. (1); Dos Aguas, U.M.M.Z. (1); 12.5 kilometers east-northeast of Dos Aguas, U.M.M.Z.

(1); Los Conejos, U.M.M.Z. (3); Uruapan, K.U. (2, 1 skeleton), U.I.M.N.H. (2); U.M.M.Z. (33, 2 skeletons, 1 tadpoles), U.S.N.M. (10). *Nayarit*: Santa Teresa, U.S.N.M. (1). 10 kilometers northeast of Ayutla, A.M.N.H. (1); Cerro San Felipe, U.I.M.N.H. (22); Huautla, A.M.N.H. (1); San Lucas Camotlán, U.S.N.M. (1). *Sinaloa*: 1.6 kilometers east of Santa Lucía, K.U. (1). *Veracruz*: No specific locality, U.S.N.M. (1); Cumbres de Acultzingo, F.M.N.H. (2), U.I.M.N.H. (5), U.S.N.M. (1).

#### *Hyla boans*

PANAMA: *Colón*: Río Candelaria, A.M.N.H. (2). *Darién*: Paya, U.U. (5); Río Tuira at Río Mono, K.U. (2). *San Blas*: Camp Sasardí, K.U. (15, 4 skeletons, 3 tadpoles, 1 eggs).

#### *Hyla bogertae*

MEXICO: *Oaxaca*: tributary of Río Atoyac, below Vivero El Tapanal, 1.6 kilometers south of La Cofradia, Distrito de Sola de Vega, L.A.C.M. (13, 1 tadpoles, 1 young).

#### *Hyla boulengeri*

NICARAGUA: No specific locality, U.S.N.M. (1). *Chontales*: 1 kilometer north, 25 kilometers west of Villa Somoza, K.U. (1). *Zelaya*: El Recreo, K.U. (2), U.M.M.Z. (1); Kanawa, A.M.N.H. (1); Sioux Plantation, A.M.N.H. (1), M.C.Z. (1); Tuli Creek, A.M.N.H. (1).

COSTA RICA: *Alajuela*: 9 kilometers north of Ciudad Quesada, U.S.C. (4); 18 kilometers north of La Florencia, U.S.C. (1); Laguna Monte Alegre, K.U. (1); Las Playuelas, 11 kilometers south of Los Chiles, U.S.C. (4); 3 kilometers northeast of Muelle de Arenal, U.S.C. (5). *Cartago*: Turrialba, K.U. (1). *Guanacaste*: Finca Taboga, 20 kilometers southeast of Las Cañas, K.U. (1), U.S.C. (1); 7 kilometers north of Liberia, U.S.C. (8); 13.6 kilometers north of Liberia, U.S.C. (3); 20.5 kilometers south of Liberia, U.S.C. (1); 4 kilometers northeast of Tilarán, U.S.C. (1); 6 kilometers northeast of Tilarán, U.M.M.Z. (1), U.S.C. (7). *Heredia*: Puerto Viejo, K.U. (44, 6 skeletons), M.C.Z. (5); 1 kilometer northeast of Puerto Viejo, U.M.M.Z. (1); 4.2 kilometers west of Puerto Viejo, K.U. (1, 1 skeleton). *Limón*: Mountain Cow Creek, near Banano, K.U. (1); Suretka, K.U. (8, 1 skeleton); Tortugero, A.M.N.H. (1). *Puntarenas*: Parrita, U.S.C. (1); 6 kilometers southwest of Rincón de Osa, K.U. (6); 4.5 kilometers southwest of Rincón de Osa, K.U. (3, 2 tadpoles) Río Rincón, 4.8 kilometers south of Bahía Rincón, U.S.C. (1); 4.4 kilometers northwest of Villa Neily, U.S.C. (1); 10.5 kilometers west-northwest of Villa Neily, K.U. (1). *San José*: 21 kilometers west-southwest of San Isidro el General, K.U. (3).

PANAMA: *Bocas del Toro*: 3.2 kilometers west of Almirante, K.U. (1). *Canal Zone*: Barro Colorado Island, A.N.S.P. (4), F.M.N.H. (1); Fort Clayton, U.I.M.N.H. (1); 2.8 kilometers southwest of Fort

Kobbe, K.U. (1); between Gatuncillo and Guayabalito, A.M.N.H. (8); Juan Mina, A.N.S.P. (1); K.U. (1), U.U. (2); 10 kilometers northwest of Miraflores Locks, A.M.N.H. (2); Road K2, T.N.H.C. (10); Road K9, T.N.H.C. (1); Summit Cardens, A.M.N.H. (1), A.N.S.P. (2), K.U. (1, 1 skeleton). *Colón*: Ciricito, C.A.S. (1); Río Gatuncillo, near Nuevo San Juan, K.U. (1). *Darién*: El Real, K.U. (3).

#### *Hyla bromeliacia*

GUATEMALA: *Alta Verapaz*: Finca Chicoyou, near Cobán, K.U. (1, 1 skeleton, 3 tadpoles, 1 eggs); Finca Samac, F.M.N.H. (1), U.M.M.Z. (6, 1 tadpoles). *El Quiché*: Finca San Francisco, U.M.M.Z. (2, 1 tadpoles).

HONDURAS: *Atlántida*: Mountains behind La Ceiba, M.C.Z. (1). *Cortés*: Mountains west of San Pedro Sula, F.M.N.H. (6), M.C.Z. (3).

#### *Hyla cadaverina*

MEXICO: *Baja California Norte*: Cañon Guadalupe, Sierra de Juárez, L.B.S.C. (2), U.M.M.Z. (11); Cañon de las Palmas, Sierra de Juárez, L.B.S.C. (2); Cañon de Llanos, 14.4 kilometers south-southwest of La Rumorosa, M.V.Z. (14); Cañon de Tajo, west side of Laguna Salada, U.M.M.Z. (3), Cañon La Providencia, east base of Sierra San Pedro Martir, U.S.N.M. (3); Ensenada U.S.N.M. (1); Isla Navidad, U.S.N.M. (1); La Laguna, Sierra La Laguna, U.S.N.M. (1). Osos Negros, U.S.N.M. (1); Playa Estero 14.4 kilometers south of Ensenada, A.M.N.H. (1); 32 kilometers east of Rosario, U.M.M.Z. (2).

#### *Hyla chaneque*

MEXICO: *Chiapas*: 5.6 kilometers south of Rayón Mescalapa, K.U. (1); 6.2 kilometers south of Rayón Mescalapa, K.U. (4, 1 skeleton), U.M.M.Z. (1). *Oaxaca*: 42.6 kilometers south of Valle Nacional, U.M.M.Z. (9); 43.5 kilometers south of Valle Nacional, U.M.M.Z. (2), K.U. (12, 2 skeletons, 3 tadpoles), M.C.Z. (5); 6 kilometers south of Campamento Vista Hermosa, K.U. (5, 2 tadpoles), U.M.M.Z. (2 tadpoles); 8 kilometers south of Campamento Vista Hermosa, K.U. (3); 11 kilometers south of Campamento Vista Hermosa, K.U. (1, 2 tadpoles); 13 kilometers south of Campamento Vista Hermosa, K.U. (1); 16 kilometers south of Campamento Vista Hermosa, K.U. (1), U.I.M.N.H. (2); Sierra Madre above Zanatepec, K.U. (1), U.I.M.N.H. (1). 8 kilometers south of Yetla, K.U. (2).

#### *Hyla charadricola*

MEXICO: *Hidalgo*: Lago de Tejocotal, 11 kilometers east of Acaxochitlán, K.U. (1), U.M.M.Z. (2); 4 kilometers southwest of Tianguistengo, K.U. (2). *Puebla*: 11.7 kilometers west of Huachinango, U.M.M.Z. (5); Río Totolapa, 14.4 kilometers west of Huachinango, K.U. (38, 3 skeletons), M.C.Z. (2), U.I.M.N.H. (1), U.M.M.Z. (5, 1 skeleton).

*Hyla chryses*

MEXICO: *Guerro*: between Puerto Chico and Asoleadero, 45 kilometers airline west-northwest of Chilpancingo, K.U. (1), U.M.M.Z. (3).

*Hyla colymba*

COSTA RICA: *Cartago*: Moravia, K.U. (2, 1 skeleton).

PANAMA: *Bocas del Toro*: La Loma, M.C.Z. (2); Río Changena, 650 meters, K.U. (1); Río Changena, 830 meters, K.U. (1 tadpoles). *Coclé*: El Valle, A.M.N.H. (1). *Darién*: Cerro Citurio, Serranía de Pirre, K.U. (1); Cerro Malí, G.M.L. (1); Laguna, K.U. (1, 1 tadpoles); Ridge between Río Jaque and Río Imamado, K.U. (2, 1 tadpoles). *Panamá*: Altos de Pacora, K.U. (1).

*Hyla crassa*

MEXICO: No specific locality, M.N.H.N. (1). *Oaxaca*: Cerro San Felipe, U.I.M.N.H. (1).

*Hyla crepitans*

HONDURAS: *Cortés*: Tela, A.M.N.H. (1).

PANAMA: *Canal Zone*: Alhajuela, U.M.M.Z. (7); Camp Chagres, K.U. (16, 1 skeleton); Fort Kobbe (1); Juan Mina, F.M.N.H. (1); junction roads K2 and K9, T.N.H.C. (19); San Pablo, A.M.N.H. (1), M.C.Z. (1), U.M.M.Z. (3); Summit Gardens, A.N.S.P. (3), F.M.N.H. (2), M.C.Z. (1). *Coclé*: El Valle, C.A.S. (1), K.U. (1). *Los Santos*: Cuanico Arriba, K.U. (1); Tonosí, K.U. (1). *Panamá*: 3 kilometers west-southwest of Chepo, K.U. (3); Chilibre, U.S.N.M. (1); Finea La Sumbadora, K.U. (3); Las Cumbres, A.M.N.H. (1); Panamá, A.M.N.H. (1), K.U. (1), M.C.Z. (2); Río Abajo, K.U. (1), U.U. (1); Río Mamoni, 5 kilometers east of Chepo, K.U. (1); 17 kilometers east of Tocumen, M.V.Z. (1).

*Hyla debilis*

COSTA RICA: *Cartago*: Tapantí, U.S.C. (15, 1 skeleton). *Heredia*: Isla Bonita, F.M.N.H. (1), K.U. (1).

PANAMA: *Bocas del Toro*: north slope of Cerro Pando, 1450 meters, K.U. (14, 2 skeletons, 4 tadpoles); Río Claro near Río Changena, K.U. (1). *Chiriquí*: Boquete, U.M.M.Z. (1).

*Hyla dendroscarta*

MEXICO: *Oaxaca*: Campamento Vista Hermosa, K.U. (4); 7.5 kilometers south of Campamento Vista Hermosa, K.U. (2). *Vera Cruz*: Barranca Metlae, M.C.Z. (1), U.I.M.N.H. (2), U.M.M.Z. (9); Cuautlapan, F.M.N.H. (1), K.U. (1), M.C.Z. (1), U.I.M.N.H. (136), U.S.N.M. (36); 12.4 kilometers southwest of Fortín de las Flores, U.M.M.Z. (4); 3 kilometers southwest of Huatusco, U.M.M.Z. (10, 1 tadpoles); Mirador, K.U. (1 tadpoles), U.M.M.Z. (3,

1 skeleton, 1 tadpoles); 3 kilometers east of San Andrés Tuxtla, K.U. (25); Sumidero, M.C.Z. (1); 15 kilometers east-northeast Tlacotepee, K.U. (1).

*Hyla ebraccata*

MEXICO: *Chiapas*: 25 kilometers south of Chontalpa, A.M.N.H. (1); 17 kilometers south of Teapa (Tabasco), U.I.M.N.H. (4). *Oaxaca*: 3 kilometers north of Donají, U.M.M.Z. (17); 21.7 kilometers south of Jesús Carranza (Veracruz), U.I.M.N.H. (2); 78 kilometers north of La Venta, T.N.H.C. (24); 43 kilometers north of Matías Romero, U.I.M.N.H. (27); 3 kilometers south of Papaloapan, A.M.N.H. (1); 3.7 kilometers north of Sarabia, U.M.M.Z. (6); 1.6 kilometers south of Toloceita, U.M.M.Z. (2); 3 kilometers south of Tolocita, K.U. (1); Ubero, U.M.M.Z. (14); 5 kilometers south of Ubero, U.M.M.Z. (1); 1.6 kilometers south of Valle Nacional, K.U. (21), U.I.M.N.H. (2). *Tabasco*: Teapa, U.M.M.Z. (15); 10 kilometers north of Teapa, U.M.M.Z. (1); 15 kilometers north of Teapa, U.M.M.Z. (7). *Vera Cruz*: 4.5 kilometers north of Aguilera, U.M.M.Z. (1); 10 kilometers south of Catemaco, U.M.M.Z. (3); Coyame, U.I.M.N.H. (6), U.M.M.Z. (7); Encinal, U.M.M.Z. (28); north side of Lago de Catemaco, K.U. (2); 25 kilometers south of Las Choapas, T.C.W.C. (19).

BRITISH HONDURAS: No specific locality, F.M.N.H. (2). *Cayo*: 16 kilometers from Belize-Cayo Road on Hummingbird Highway. U.M.M.Z. (1); Cohune Ridge, M.C.Z. (1), U.M.M.Z. (18); 5 kilometers from Millionaro Camp on Pine Ridge Road, U.M.M.Z. (6). *Stann Creek*: Hummingbird Highway between Roaring Creek and Stann Creek, U.M.M.Z. (2).

GUATEMALA: *El Petén*: 8 kilometers south of La Libertad, U.S.N.M. (5); Posa de Jieotea, 8 kilometers south of Piedras Negras, U.I.M.N.H. (2); Tooeog, 15 kilometers southeast of La Libertad, K.U. (56, 10 skeletons, 2 eggs, 2 tadpoles); Yaxha, U.M.M.Z. (1).

NICARAGUA: *Matagalpa*: 2 kilometers north, 6 kilometers east of Esquipulas, K.U. (1). *Zelaya*: Machuea, A.N.S.P. (1).

COSTA RICA: *Alajuela*: Las Playuelas, 11 kilometers south of Los Chiles, U.S.C. (1). *Cartago*: Lago Bonilla, K.U. (6, 2 skeletons); Moravia de Turrialba, K.U. (22, 4 skeletons, 1 eggs), U.S.C. (12); 11 kilometers southwest of Moravia de Turrialba, K.U. (1); 1 kilometer east-northeast of Pacuare, K.U. (48); 2 kilometers south of Paraiso, U.S.C. (17); Turrialba, F.M.N.H. (56), K.U. (91, 5 skeletons), M.C.Z. (1), U.M.M.Z. (14), U.S.C. (45), U.S.N.M. (8). *Guanacaste*: Finea San Boso, U.S.C. (37); Laguna Arenal, U.S.C. (1); Silencio, U.S.C. (42); Tilarán, K.U. (38); 2 kilometers east of Tilarán, K.U. (20, 1 eggs, 1 tadpoles), U.S.C. (9). *Heredia*: Finca La Selva, U.S.C. (3); Puerto Viejo, K.U. (13, 3 tadpoles). *Limón*: Bambú, U.S.C. (2); Cuácimo, U.S.C. (1); Limón, A.M.N.H. (4); Los Diamantes, F.M.N.H. (2); Suretka, K.U. (1, 2 skeletons), M.C.Z. (2). *Puntarenas*: 1.6 kilometers south of Agua Buena,



U.S.C. (2); 5 kilometers west-northwest of Barranea, U.M.M.Z. (5); 3 kilometers northeast of Boca de Barranea, U.S.C. (1); 12 kilometers west-northwest of Esparta, K.U. (1); Esquinas Forest Preserve, between Palmar and Goltito, K.U. (1); 3 kilometers east of Goltito, K.U. (2); Palmar, K.U. (1); 3 kilometers southeast of Palmar Norte, K.U. (1); 4 kilometers east-southeast of Palmar Norte, K.U. (2); 3 kilometers northwest of Piedras Blancas, K.U. (1); Rincón de Osa, U.M.M.Z. (6), U.S.C. (7); 4.5 kilometers west of Rincón de Osa, K.U. (26); 6 kilometers southwest of Rincón de Osa, K.U. (10); Río Ferruviosa, 7 kilometers south of Rincón de Osa, U.S.C. (12); 7 kilometers west of Villa Neily, U.S.C. (1); 10.5 kilometers west-northwest of Villa Neilly, K.U. (5, 2 skeletons).

PANAMA: *Bocas del Toro*: 2.5 kilometers west of Almirante, U.U. (2); 3.2 kilometers northwest of Almirante, K.U. (4); Isla Bastimentos, K.U. (1). *Canal Zone*: No specific locality, T.N.H.C. (90); between Catuncillo and Guayabilito, A.M.N.H. (17); Juan Mina, U.U. (4); Río Chagres, near Gamboa, U.M.M.Z. (1); Summit, K.U. (5), M.C.Z. (1). *Chiriquí*: Progreso, U.M.M.Z. (2). *Coclé*: El Valle, A.M.N.H. (13), F.M.N.H. (1), K.U. (1), M.V.Z. (3). *Colón*: Achote K.U. (67, 4 skeletons); Cirieito, C.A.S. (4). *Darién*: Camp Townsend, Río Chucunaque, A.M.N.H. (1); Laguna, K.U. (2); Río Tuira at Río Mono, K.U. (23, 4 skeletons); Río Ucurgantí, 7 kilometers above mouth, K.U. (2); Tacareuna, K.U. (40, 1 tadpoles). *Panamá*: south slope of Cerro La Campana, F.M.N.H. (17), K.U. (17); 3 kilometers west-southwest of Chepo, K.U. (3); Tapia, A.M.N.H. (1); 33 kilometers east of Tocumen, M.V.Z. (3). *San Blas*: Sasardí, K.U. (1).

#### *Hyla echinata*

MEXICO: Oaxaca: Vista Hermosa, U.I.M.N.H. (1), U.M.M.Z. (1).

#### *Hyla elaeochroa*

NICARAGUA: No specific locality, U.S.N.M. (1). *Boaco*: 14 kilometers north, 13 kilometers east of Boaco, K.U. (1). *Chontales*: 1 kilometer north, 2.5 kilometers west of Villa Somoza, K.U. (13). *Nueva Segovia*: 5 kilometers north, 2.5 kilometers east of Jalapa, K.U. (2). *Zelaya*: Cukra, A.M.N.H. (1); El Reereo, U.M.M.Z. (1); Tuli Creek, A.M.N.H. (2).

COSTA RICA: *Alajuela*: 9 kilometers north of Ciudad Quesada, U.S.C. (5); Laguna Monte Alegre, K.U. (1); Las Vegas, 8 kilometers south of Tanque, U.S.C. (5); Los Chiles, A.M.N.H. (1). *Cartago*: Cervantes, U.S.C. (1); Chitaría, A.N.S.P. (1), 2 kilometers east of Chitaría, K.U. (1); El Sileneio, 14.4 kilometers northeast of Turrialba, K.U. (2); Juan Vinas, U.S.C. (1); 9 kilometers from La Suiza, U.S.C. (18); 4.6 kilometers east-northeast of Paeuare, K.U. (35); 4 kilometers south of Pavones, K.U. (1); Peralta, K.U. (6); Turrialba, F.M.N.H. (33), K.U. (146, 19 skeletons, 2 tadpoles, 1 eggs), M.C.Z. (1),

T.N.H.C. (1), U.M.M.Z. (12), U.S.C. (174); 5 kilometers south of Turrialba, U.I.M.N.H. (1). *Guana-caste*: 2 kilometers east of Tilarán, K.U. (22, 2 tadpoles). *Heredia*: Finca La Selva, U.M.M.Z. (1); Puerto Viejo, K.U. (27, 11 skeletons, 7 tadpoles), M.C.Z. (2), U.M.M.Z. (1). *Limón*: Bambú, U.S.C. (2); Batán, K.U. (10); La Castilla, Río Reventazón, A.N.S.P. (7); La Lola, K.U. (21, 2 skeletons), U.M.M.Z. (3, 1 tadpoles); Limón, K.U. (8); Los Diamantes, K.U. (2), U.M.M.Z. (11); 2.5 kilometers east of Los Diamantes, U.S.C. (8); Pandora, U.M.M.Z. (4), U.S.C. (1); Portete, U.M.M.Z. (5); Sipurio, U.S.N.M. (1); Suretka, K.U. (16, 1 skeleton); Tortuguero, M.C.Z. (1), U.F. (10); Zent, M.C.Z. (4). *Puntarenas*: 5 kilometers northwest of Buenos Aires, K.U. (1); 10 kilometers east of Esparta, K.U. (1 tadpoles); Goltito, K.U. (3), U.M.M.Z. (2); 3 kilometers southeast of Goltito, U.S.C. (4); Gromaeo, U.M.M.Z. (1); 2.5 kilometers southeast of Palmar Sur, K.U. (9); 4 kilometers southeast of Palmar Sur, K.U. (2 tadpoles); 10.7 kilometers southeast of Palmar Sur, K.U. (1 skeleton); 13 kilometers southeast of Palmar Sur, K.U. (3, 1 eggs, 4 tadpoles); Parrita, U.S.C. (9); 3 kilometers northwest of Piedras Blancas, K.U. (14); 10 kilometers northwest of Piedras Blancas, K.U. (14); 11 kilometers north, 3 kilometers west of Puntarenas, T.C.W.C. (7); Quebrada Boruca, 22 kilometers east of Palmar Norte, K.U. (1); Rincón de Osa, K.U. (15); 4.5 kilometers west of Rincón de Osa, K.U. (19, 1 tadpoles); Río Zapote, 8 kilometers east of Palmar Norte, K.U. (1).

PANAMA: *Bocas del Toro*: Almirante, K.U. (1), U.S.N.M. (1); 3 kilometers west of Almirante, K.U. (1), U.U. (1); Isla Bastimentos, K.U. (4); Río Criamola, 3.7 kilometers from mouth, K.U. (1); Río San San, M.C.Z. (2). *Chiriquí*: Puerto Armuelles, A.N.S.P. (1); Progreso, U.M.M.Z. (6); Río Garichine, 8.3 kilometers east-southeast of Paso de Canoas, K.U. (2).

#### *Hyla erythromma*

MEXICO: *Guerrero*: Acahuitzotla, T.C.W.C. (1); Agua del Obispo, F.M.N.H. (1), K.U. (1, 2 tadpoles), T.C.W.C. (1), U.M.M.Z. (5); 1.6 kilometers east of San Andreas de la Cruz, K.U. (2); 3.3 kilometers north of San Vicente, K.U. (5). *Oaxaca*: 5 kilometers S. Yetla, K.U. (6); 6.9 kilometers south of Yetla, K.U. (1); 8 kilometers south of Yetla, K.U. (51, 2 skeletons, 5 tadpoles, 1 eggs); U.I.M.N.H. (4).

#### *Hyla euphorbiacea*

MEXICO: *Oaxaca*: Camotlán, A.M.N.H. (2); Cañon Tlatixtae, 6.4 kilometers E. Oaxaca, A.M.N.H. (1); Cerro San Felipe, U.I.M.N.H. (26); South slope of Cerro Maehín, K.U. (1 tadpoles); El Punto, A.M.N.H. (1 tadpoles), 1.6 kilometers north of El Punto, A.M.N.H. (3, 1 tadpoles); 3 kilometers north of El Punto, A.M.N.H. (2); Cuelatao, U.M.M.Z. (1); 25 kilometers north of Cuelatao, K.U. (1); Ixtlán de Juárez, U.M.M.Z. (91); 16 kilometers south of Ixtlán de Juárez, U.I.M.N.H. (5); 17 kilometers south of

Ixtlán de Juárez, U.M.M.Z. (9); 20 kilometers south of Ixtlán de Juárez, U.I.M.N.H. (26); 27 kilometers south of Ixtlán de Juárez, U.M.M.Z. (5); 29 kilometers south of Ixtlán de Juárez, U.I.M.N.H. (62); Lachigola, A.M.N.H. (27); Llano de las Flores, A.M.N.H. (4, 1 skeleton), K.U. (89, 10 skeletons), U.I.M.N.H. (19), U.M.M.Z. (87); Oaxaca, A.M.N.H. (1); U.I.M.N.H. (3), U.M.M.Z. (18), U.S.N.M. (1); 5 kilometers northeast of Oaxaca, U.F. (5); 1.6 kilometers east of Oaxaca, U.I.M.N.H. (42); 2.7 kilometers southeast of Oaxaca, U.M.M.Z. (16); 4 kilometers southeast of Oaxaca, K.U. (12, 1 tadpoles, 1 eggs); 5 kilometers southeast of Oaxaca, U.M.M.Z. (11); 6 kilometers southeast of Oaxaca, K.U. (12); 8 kilometers southeast of Oaxaca, K.U. (49, 3 skeletons), U.M.M.Z. (7); 15 kilometers southeast Oaxaca, U.M.M.Z. (7); 4 kilometers west of Oaxaca, U.M.M.Z. (7); 14.4 kilometers northwest of Oaxaca, U.M.M.Z. (6); between Oaxaca and Tlacolula, U.I.M.N.H. (4); San Andres Chichahuastla, U.I.M.N.H. (1); 3 kilometers northeast of San Andrés Chichahuastla, U.M.M.Z. (27); San Felipe, A.M.N.H. (1); 1.6 kilometers south of San Felipe Ixtapa, U.I.M.N.H. (3); 3 kilometers east of Santa Lucia, A.M.N.H. (10); Santo Domingo Ocoteppec, U.I.M.N.H. (4); San Vicente Lachixio, K.U. (1); 4 kilometers southeast of Tlacolula, T.N.H.C. (8); 15 kilometers north of Tlaxiaco, K.U. (1 tadpoles). *Puebla*: Paraje Verde, U.I.M.N.H. (3); U.M.M.Z. (1); Puente Colorado, U.M.M.Z. (2). *Veracruz*: Cumbres de Acultzingo, I.P.N. (1), K.U. (5), M.C.Z. (1), U.I.M.N.H. (17), U.M.M.Z. (19), U.S.N.M. (11).

GUATEMALA: *Alta Verapaz*: Cobán, F.M.N.H. (3); Finca Samac, U.M.M.Z. (1).

#### *Hyla eximia*

MEXICO: *Aguascalientes*: 13 kilometers east of Aguascalientes, F.M.N.H. (10), U.I.M.N.H. (15); 16 kilometers east of Aguascalientes, F.M.N.H. (20), U.I.M.N.H. (18); 4 kilometers east of Cañada Honda, S.U. (1); 8 kilometers north of Rincón de Romos, U.M.M.Z. (1); 30 kilometers south of Rincón de Romos, U.I.M.N.H. (2). *Chihuahua*: No specific locality, M.C.Z. (1); Colonia García, U.S.N.M. (3); 26 kilometers south, 21 kilometers west of Creel, K.U. (2); 37 kilometers south, 2.5 kilometers east of Creel, K.U. (16); Meadow Valley, U.S.N.M. (6); Mojara-chic, F.M.N.H. (1), U.I.M.N.H. (2), U.M.M.Z. (1); 3 kilometers west of Samachique, K.U. (1); 3 kilometers southwest of San José de Babicora, K.U. (22); 5 kilometers northeast of Temoris, K.U. (1). *Distrito Federal*: Atzacualco, U.S.N.M. (1); Ciudad México, I.P.N. (1), U.S.N.M. (2); Contreras, U.M.M.Z. (1); Guadalupe, A.M.N.H. (15); Lago Texcoco, U.M.M.Z. (7); 1.6 kilometers west of Nalpan, A.M.N.H. (37); Parque Chapultepec, A.M.N.H. (1); Pedregal de San Angel, I.P.N. (16); San Juanico, A.M.N.H. (1); San Luis, 10 kilometers east of Xochimilco, U.M.M.Z. (4); San Mateo Chalpa, A.M.N.H. (1); 1.6 kilometers southwest of Ticomán, A.M.N.H. (4); Tlalpan, F.M.N.H. (2); Valle de México, U.S.N.M. (1); Xochimilco, A.M.N.H. (15), A.N.S.P. (3), I.P.N. (7),

U.M.M.Z. (1); 1.6 kilometers southwest of Xochimilco, U.M.M.Z. (1). *Durango*: Buenos Aires, 6 kilometers southwest of La Ciudad, A.M.N.H. (29), K.U. (1 tadpoles); Coyotes, F.M.N.H. (1), U.M.M.Z. (4); Cerro Huehuento, 40 kilometers north-northwest of El Salto, U.M.M.Z. (1); Durango, M.C.Z. (1), U.M.M.Z. (12); Río Mezquital, 16 kilometers north of Durango, U.I.M.N.H. (21); 24 kilometers north of Durango, U.I.M.N.H. (3); 20 kilometers east of Durango, U.M.M.Z. (5); 96 kilometers west of Durango, M.C.Z. (2); 14 kilometers east of El Espinosa, L.B.S.C. (1); El Salto, A.N.S.P. (2), K.U. (2); 4 kilometers northeast of El Salto, U.I.M.N.H. (33); 16 kilometers northeast of El Salto, U.I.M.N.H. (3); 2 kilometers southwest of El Salto, I.P.N. (8); 11.3 kilometers southwest of El Salto, U.I.M.N.H. (1); 14 kilometers southwest of El Salto, K.U. (8), U.I.M.N.H. (3); 16 kilometers southwest of El Salto, C.A.S. (1), K.U. (17); 23 kilometers southwest of El Salto, U.M.M.Z. (7); 44.3 kilometers southwest of El Salto, K.U. (3); 49 kilometers southwest of El Salto, U.I.M.N.H. (1); 53 kilometers southwest of El Salto, L.B.S.C. (46); Laguna del Progreso, U.M.M.Z. (20); 7 kilometers northeast of Las Adjuntas, U.I.M.N.H. (1); 4 kilometers southwest of Las Adjuntas, U.I.M.N.H. (4); 19 kilometers southwest of Las Adjuntas, K.U. (13); 8 kilometers north of Morcillo, U.M.M.Z. (3); Pueblo Nuevo, A.N.S.P. (2), U.M.M.Z. (12); Río Mezquital, 16 kilometers northeast of Durango, U.I.M.N.H. (1). *Guanajuato*: No specific locality, U.S.N.M. (3); Acambaro, F.M.N.H. (4); Celaya, F.M.N.H. (1); 11 kilometers northwest of León, U.I.M.N.H. (18); 10 kilometers west of Panjamo, U.I.M.N.H. (2); Silao, U.S.N.M. (1); 22 kilometers south of Valle de Santiago, U.I.M.N.H. (63). *Guerrero*: 4 kilometers southwest of Ahmolonga, K.U. (3). T.C.W.C. (20), U.M.M.Z. (6); East of Chilapa, K.U. (1). Chilpancingo, M.C.Z. (1); 22 kilometers south of Chilpancingo, C.A.S. (1); 22 kilometers south of Ixtapán de la Sal (Mexico), K.U. (17); Omiltemi, M.C.Z. (1), T.C.W.C. (5); U.I.M.N.H. (10), U.S.N.M. (3); 3 kilometers north of Omiltemi, T.C.W.C. (1); 6 kilometers north of Omiltemi, U.S.N.M. (2); 10 kilometers east of Omiltemi, F.M.N.H. (3); 3 kilometers west of Omiltemi, T.C.W.C. (9); Tixtla, F.M.N.H. (1), U.I.M.N.H. (1). *Hidalgo*: 10 kilometers east of Acaxochitlán, A.M.N.H. (1); 5.6 kilometers west Acaxochitlán, U.M.M.Z. (6); Agua Blanca, near Apulca, U.M.M.Z. (1); 16 kilometers north of Agua Blanca, U.M.M.Z. (6); 16 kilometers south of Apulca, U.M.M.Z. (15); Atotonilco Grande, F.M.N.H. (32), U.I.M.N.H. (24); El Chico Parque Nacional, A.M.N.H. (8); Guerrero, M.C.Z. (3); 20 kilometers west-southwest of Huachinango (Puebla), U.M.M.Z. (2); Jacala, U.M.M.Z. (2); Lago Tejocotal, I.P.N. (1), U.M.M.Z. (1); 2.5 kilometers southwest of Tianguistengo, K.U. (2); 6 kilometers Tianguistengo, F.M.N.H. (4); 5 kilometers northwest of Tianguistengo, U.I.M.N.H. (1); 13 kilometers east-northeast of Tulancingo, U.M.M.Z. (1); 10 kilometers southwest of Tulancingo, U.M.M.Z. (2); 15 kilometers southwest of Tulancingo, U.M.M.Z.



- (1); Velasco, A.M.N.H. (2); 6 kilometers south of Zacualtipán, F.M.N.H. (11), U.I.M.N.H. (12). *Jalisco*: Agua Delgada, 6 kilometers north of Cuadaluja, A.M.N.H. (14); 3 kilometers east of Ajijic, A.M.N.H. (1); 5 kilometers west of Arandes, K.U. (45); Atemajae, A.M.N.H. (2); Atotonilco del Alto, K.U. (4); Autlán Road, F.M.N.H. (2); 5 kilometers northeast of Autlán, F.M.N.H. (1), U.I.M.N.H. (2); 4 kilometers west of Ayo el Chico, U.I.M.N.H. (11); Cerro de la Venta, 22 kilometers west-northwest of Cuadaluja, K.U. (1); Chapala, A.M.N.H. (1 tadpoles), F.M.N.H. (7), U.I.M.N.H. (10); 11.5 kilometers north of Chapala, U.I.M.N.H. (11); 16 kilometers north of Chapala, A.M.N.H. (1); 3 kilometers north of Ciudad Cuzmán, U.M.M.Z. (5); 5 kilometers northeast of Ciudad Cuzmán, F.M.N.H. (6); 1.6 kilometers west of Ciudad Cuzmán, U.M.M.Z. (2); Cuarente, K.U. (1); 5 kilometers northwest of Degollado, K.U. (3); Cuadaluja, A.M.N.H. (2); F.M.N.H. (3), K.U. (1); U.I.M.N.H. (1); 20 kilometers south, 29 kilometers west of Cuadaluja, K.U. (1); 21 kilometers south of Cuadaluja, U.M.M.Z. (2); 38 kilometers south of Cuadaluja, U.M.M.Z. (1); 29 kilometers southwest of Cuadaluja, U.M.M.Z. (19); 1 kilometer northwest of Ixtlahuacán, A.M.N.H. (24); 8 kilometers northwest of Ixtlahuacán, A.M.N.H. (1); 1.6 kilometers south of Jalostotlán, K.U. (1); Jamay, A.M.N.H. (11); 3 kilometers east of Jocotepec, U.I.M.N.H. (1); 5 kilometers northwest of Jocotepec, A.M.N.H. (2), U.I.M.N.H. (2), U.S.N.M. (2); Lago Chapala, A.M.N.H. (2); Lagos de Morena, A.M.N.H. (1), C.A.S. (1); 13 kilometers northeast of Lagos de Morena, U.I.M.N.H. (6); 40 kilometers east of Lagos de Morena, K.U. (16, 2 skeletons, 1 tadpoles); 3 kilometers west-northwest of Lagos de Morena, K.U. (2); Laguna de Magdalena, A.M.N.H. (1); La Mesa María de León, K.U. (39); 3 kilometers northwest of Magdalena, K.U. (1), T.N.H.C. (1); 1.6 kilometers northwest of Mazamitla, U.M.M.Z. (1); Ocotlán, A.M.N.H. (1); 21.7 kilometers west of Ojuelos, U.I.M.N.H. (3); Rancho Primavera, near Cuadaluja, U.I.M.N.H. (1); 5 kilometers west of San Antonio, U.I.M.N.H. (1); 35 kilometers west of Soyatlán, T.C.W.C. (10); 10 kilometers north, 6 kilometers east of Tepatitlán, K.U. (15); 12 kilometers northeast of Tepatitlán, U.M.M.Z. (17); Tlaquepaque, A.M.N.H. (14); Tonolá, A.M.N.H. (3); between Tonolá and Tlaquepaque, A.M.N.H. (5); Villa Corona, north end of Lago Atotonilco, K.U. (21); Villa de Cuadalupe, C.A.S. (1); 1.6 kilometers northeast of Villa Hidalgo, K.U. (3); 11 kilometers south, 1.6 kilometers east of Yahualica, K.U. (1); Zapotiltic, F.M.N.H. (4), U.I.M.N.H. (3). *México*: 5.1 kilometers south of Acolmán, T.N.H.C. (3); Ameyal, U.I.M.N.H. (5); 5 kilometers south of Bosconcheve, U.M.M.Z. (32); Chalco, F.M.N.H. (1); Chapingo, I.P.N. (1); 45 kilometers west of Ciudad Mexico, T.C.W.C. (2); Ixtapán de la Sal, A.M.N.H. (11), F.M.N.H. (3), T.N.H.C. (11); 5 kilometers north of Ixtapán de la Sal, T.N.H.C. (2); 6 kilometers north of Ixtapán de la Sal, U.M.M.Z. (23, 2 tadpoles); Laguna Agua Buena, 27 kilometers southwest of Toluca, U.M.M.Z. (6); Laguna de Ojuelos, 8 kilometers west of Toluca, A.M.N.H. (3); La Marquesa, I.P.N. (1); Lengua de Vaca, 16 kilometers east of Zitacuaro (Michoacán), U.M.M.Z. (1); Lerma, F.M.N.H. (2), U.I.M.N.H. (2); Nevada de Toluca, F.M.N.H. (2), U.I.M.N.H. (2); Rancho Cuadalupe, 51 kilometers west of Toluca, U.I.M.N.H. (1); Río Frio, U.I.M.N.H. (1); 5 kilometers north, 11 kilometers west of San José Allende, K.U. (1); San Juan Teotihuacán, M.C.Z. (1); 16 kilometers from San Martín, F.M.N.H. (1); U.I.M.N.H. (1); 8 kilometers south of Tenancingo, K.U. (2); 5.6 kilometers south of Tenango, T.C.W.C. (10); 6 kilometers west of Tepexpan, U.M.M.Z. (15); Toluca, A.M.N.H. (1), F.M.N.H. (1), U.S.N.M. (1); 3 kilometers west of Toluca, F.M.N.H. (10); 24-32 kilometers west of Toluca, U.M.M.Z. (1); 10 kilometers north-northwest of Toluca, F.M.N.H. (3); Tonatico, I.P.N. (1); 1.6 kilometers south of Valle de Bravo, K.U. (4); 19 kilometers west of Villa Victoria, U.S.N.M. (4). *Michoacán*: 11 kilometers west of Ciudad Hidalgo, U.M.M.Z. (36); Cojumatlán, F.M.N.H. (1), U.I.M.N.H. (1); 6 kilometers north of Copuyo, T.C.W.C. (4); 6 kilometers south of Cuitzeo, U.M.M.Z. (1); 30 kilometers north of Jacona, U.I.M.N.H. (1); Jiquilpan, U.I.M.N.H. (1), U.M.M.Z. (1); 8.3 kilometers east-southeast of Jiquilpan, T.N.H.C. (1); Lago de Camécuaro, U.M.M.Z. (1); Lago de Pátzcuaro, A.M.N.H. (7), F.M.N.H. (2), U.I.M.N.H. (1); 2.5 kilometers south of Los Reyes, K.U. (1); Morelia, F.M.N.H. (1); 11 kilometers west of Morelia, A.M.N.H. (9); Pátzcuaro, A.M.N.H. (6); 10 kilometers north of Pátzcuaro, U.I.M.N.H. (92); 3 kilometers northeast of Pátzcuaro, T.N.H.C. (1); 8 kilometers northeast of Pátzcuaro, U.M.M.Z. (6); 5 kilometers south of Pátzcuaro, C.A.S. (1); 25 kilometers south of Pátzcuaro, U.M.M.Z. (3); Sahuayo, U.S.N.M. (3); 5 kilometers west of Tangamandapio, U.M.M.Z. (4); Temascal, I.P.N. (1); 3 kilometers west of Temascal, U.M.M.Z. (36); Tupatario, U.S.N.M. (1); Tuxpan, U.M.M.Z. (15); 25 kilometers west of Tuxpan, U.I.M.N.H. (3); between Tzintzuntzan and Pátzcuaro, U.M.M.Z. (25); Undameo, U.M.M.Z. (2); Uruapan, F.M.N.H. (6), U.I.M.N.H. (4); Villamor, A.M.N.H. (2); Zacapu, U.I.M.N.H. (1); Zamora, C.A.S. (1), F.M.N.H. (2), U.I.M.N.H. (1); 1.6 kilometers southeast of Zamora, T.N.H.C. (2); 14.4 kilometers east of Zamora, U.M.M.Z. (22); 1.6 kilometers northeast of Zinapécuaro, K.U. (10). *Morelos*: 18 kilometers southeast of Cuautla, T.N.H.C. (4); 1.6 kilometers northwest of Cuautlixco, U.M.M.Z. (1); 5 kilometers northwest of Cuautlixco, U.M.M.Z. (5); 3.5 kilometers west of Cuautlixco, (3); Cuernavaca, F.M.N.H. (2), T.C.W.C. (9), U.I.M.N.H. (5); 2.7 kilometers east of Cuernavaca, T.N.H.C. (1); 5.6 kilometers south of Cuernavaca, F.M.N.H. (1); 2 kilometers south of Jonacatepec, T.C.W.C. (9); Progreso, T.C.W.C. (30), U.F. (10); Temisco, F.M.N.H. (1), U.I.M.N.H. (2); Tepoztlán, F.M.N.H. (3). *Nayarit*: 3 kilometers south of Acaponeta, U.M.M.Z. (1); Arroyo de Riflón, 9 kilometers north of Compostela, L.B.S.C. (1); 13 kilometers north of Compostela, L.B.S.C. (1); 3 kilometers south of Compostela, K.U. (1); Ixtlán del Río,



U.M.M.Z. (1); 3 kilometers northwest of Ixtlán del Río, T.C.W.C. (3); Laguna San Pedro, 16 kilometers east of Compostela, A.M.N.H. (3); Petaquilla, A.M.N.H. (4); Río San Cayetano, 5.6 kilometers southeast of Tepic, A.M.N.H. (2); Santa Teresa, U.S.N.M. (4); Tepic, F.M.N.H. (6); S.U. (2), U.I.M.N.H. (3), U.M.M.Z. (2 tadpoles), U.S.N.M. (2); 19 kilometers southeast of Tepic, K.U. (2); 22 kilometers southeast of Tepic, A.M.N.H. (2); 8.6 kilometers south-southeast of Tepic, U.M.M.Z. (14); 32 kilometers south-southeast, 6 kilometers east of Tepic, L.B.S.C. (1); 37 kilometers south-southeast of Tepic, L.B.S.C. (3); 6 kilometers south of Tepic, L.B.S.C. (1); 8 kilometers south of Tepic, L.B.S.C. (2); 8.8 kilometers south of Tepic, A.M.N.H. (1); 10 kilometers south of Tepic, L.B.S.C. (12); 35 kilometers south of Tepic, L.B.S.C. (3). *Puebla*: 2 kilometers south of Ahuazotepec, U.I.M.N.H. (5); 6 kilometers south of Amazoc, F.M.N.H. (13), U.I.M.N.H. (10); 3 kilometers north of Cholula, F.M.N.H. (10), U.I.M.N.H. (11); 17 kilometers southeast of Huachinango, T.C.W.C. (1); 16 kilometers southwest of Huachinango, A.M.N.H. (1); 5.6 kilometers west of Huachinango, U.M.M.Z. (17, 1 tadpoles); 10 kilometers southwest of Izúcar de Matamoros, K.U. (1); Los Molinos, U.M.M.Z. (2); Puebla, A.M.N.H. (1), U.S.N.M. (1); 11 kilometers south, 5 kilometers east of Puebla, K.U. (2); 1.6 kilometers southwest of Puebla, U.M.M.Z. (19); 4.2 kilometers southwest of Puebla, U.M.M.Z. (3); 6 kilometers southwest of Puebla, U.M.M.Z. (21); Reyes, near Santa Catarina, A.M.N.H. (1); Santa Catarina, A.M.N.H. (1); Tepeaca, F.M.N.H. (1), U.I.M.N.H. (2); 9 kilometers south of Tepeojuma, U.M.M.Z. (1); Tezuitlán, U.S.N.M. (1). *Querétaro*: 4 kilometers north of Querétaro, U.I.M.N.H. (1); 13 kilometers northwest of Querétaro, K.U. (20); 1.6 kilometers south of Santa Rosa, U.I.M.N.H. (2). *San Luis Potosí*: Alvarez, M.C.Z. (2), mountains north of Alvarez, M.C.Z. (1); 38 kilometers east of San Luis Potosí, U.M.M.Z. (12). *Tamaulipas*: La Joya de Salas, U.M.M.Z. (43). *TLaxcala*: Apizaco, U.I.M.N.H. (20), U.M.M.Z. (18); Atlahuatzia, 10 kilometers northeast of Tlaxcala, U.I.M.N.H. (4); 1 kilometer northwest of Ocotoxco, U.I.M.N.H. (3); 5 kilometers northwest of Sanctorium, T.N.H.C. (3); 3 kilometers south of San Ildefonso Hueyotlipan, U.I.M.N.H. (1). *Veracruz*: Banderilla, U.I.M.N.H. (1); Cuautlapan, K.U. (2); Jacales, K.U. (2); 10 kilometers southwest of Jacales, K.U. (69); Las Vigas, U.M.M.Z. (1); Mirador, U.S.N.M. (3); Tierra Colorada, U.I.M.N.H. (1); ?Volcán San Martín, U.I.M.N.H. (2); Nuchil, F.M.N.H. (1). *Zacatecas*: 16.6 kilometers northwest of Jalpa, K.U. (2); 9.6 kilometers east of Monte Escobedo, K.U. (2); 5 kilometers northwest of Teul, U.M.M.Z. (11).

#### *Hyla fimbrinembra*

COSTA RICA: *Alajuela*: Cinchona, R.C.T. (1). *Heredia*: Isla Bonita, R.C.T. (1).

#### *Hyla godmani*

MEXICO: *Puebla*: María Andrea, A.M.N.H. (8); 10 kilometers southwest of Mecatepec (Veracruz), U.I.M.N.H. (13). *Veracruz*: 5 kilometers east-southeast of Córdoba, A.M.N.H. (7), K.U. (2 tadpoles), T.N.H.C. (10); 7.2 kilometers east-southeast of Córdoba, K.U. (1); U.M.M.Z. (22); 6.4 kilometers east of Encero, A.M.N.H. (1), F.M.N.H. (1), S.U. (1), U.I.M.N.H. (18); Jalapa, U.M.M.Z. (2); 23 kilometers southeast of Jalapa, K.U. (13, 2 skeletons), 2 kilometers east-northeast of Mata Oscura, K.U. (34, 13 skeletons); Mirador, U.M.M.Z. (1); Misantla, B.M.N.H. (1); Palma Sola, U.S.N.M. (20); Potrero Viejo, F.M.N.H. (5), M.C.Z. (14), U.I.M.N.H. (48), U.M.M.Z. (16); 37 kilometers west of Posa Rica, U.M.M.Z. (3).

#### *Hyla hazelae*

MEXICO: *Oaxaca*: Cañon Tlalixtae, 6 kilometers southeast, 17 kilometers northeast of Oaxaca, K.U. (1); Cerro Machín, U.I.M.N.H. (3); Cerro San Felipe, F.M.N.H. (4), U.S.N.M. (2); 3 kilometers east of Ixtlán de Juárez, A.M.N.H. (1); 13 kilometers northwest of Ixtlán de Juárez, T.N.H.C. (4) near Oaxaca, U.I.M.N.H. (2); 2 kilometers south of E. Punto, K.U. (2, 1 skull).

#### *Hyla lancasteri*

COSTA RICA: *Cartago*: 7.4 kilometers west of Juan Vina, U.M.M.Z. (1); Moravia, K.U. (46, 3 skeletons), U.S.C. (2); 3 kilometers south of Pavones, K.U. (65, 2 skeletons, 3 tadpoles). U.M.M.Z. (5), U.S.C. (7); Peralta, M.C.Z. (1); Río Chitaría, 3 kilometers north-northeast of Pavones, K.U. (2), M.C.Z. (1), U.S.C. (5); Turrialba, K.U. (9, 1 skeleton), M.C.Z. (2); south slope of Volcán Turrialba, U.M.M.Z. (5 tadpoles). *Limón*: El Tigre, 9-14 kilometers southwest of Siquirres, U.S.C. (4).

PANAMA: *Bocas del Toro*: North slope of Cerro Pando, 1450 meters, K.U. (21, 2 skeletons, 3 tadpoles, 1 eggs); north slope of Cerro Pando, 1810 meters, K.U. (2); north slope of Cerro Pando, 1920 meters, K.U. (9, 1 eggs); Río Changena, 650 meters, K.U. (2); Río Changena, 830 meters, K.U. (8); Río Clara near junction with Río Changena, 910 meters, K.U. (3, 4 tadpoles, 1 eggs).

#### *Hyla legleri*

COSTA RICA: *Puntarenas*: Finca El Heleehales, 15 kilometers northeast of Potrero Grande, U.S.C. (2); Finca Loma Linda, 2 kilometers south-southwest of Cañas Gordas, U.M.M.Z. (4), U.S.C. (20). *San José*: south slope Cerro de la Muerte, 1540 meters, U.S.C. (3); 14 kilometers north of San Isidro el General, K.U. (2, 3 skeletons), U.M.M.Z. (1); 15 kilometers north of San Isidro el General, K.U. (2, 1 tadpoles); 15 kilometers west-southwest of San Isidro el General, K.U. (12, 5 tadpoles), U.S.C. (6), U.M.M.Z. (1).

PANAMA: *Chiriquí*: Finca Santa Clara, K.U. (3, 1 tadpoles).

*Hyla loquax*

MEXICO: *Campeche*: Laguna Alvarado, 65 kilometers south of Xpujil, K.U. (21); 10 kilometers east of Laguna Silvituc, K.U. (2); Tres Brazos, F.M.N.H. (1), U.I.M.N.H. (1). *Chiapas*: El Suspiro, U.M.M.Z. (1); Laguna Ocotal, M.C.Z. (1); 16 kilometers south of Teapa (Tabasco), U.I.M.N.H. (6). *Oaxaca*: 3.7 kilometers north of Donaji, U.M.M.Z. (7); 43 kilometers north of Matías Romero, U.I.M.N.H. (21); Río Chicapa, near El Atravesado, A.M.N.H. (1). *Tabasco*: Teapa, T.N.H.C. (4); 12.4 kilometers north of Teapa, U.M.M.Z. (2); 27 kilometers north of Teapa, U.M.M.Z. (10); 3.5 kilometers south of Villahermosa, U.M.M.Z. (16). *Veracruz*: 19 kilometers north of Acayucan, U.I.M.N.H. (4); 4.5 kilometers south of Aquilera, U.M.M.Z. (3); Cuautotlapam, U.M.M.Z. (3); 8 kilometers southwest of Coatzacoalcas, U.M.M.Z. (36); Encinal, U.M.M.Z. (4); 5 kilometers west of Juan Díaz Covarrubias, U.M.M.Z. (8); 8 kilometers south of Lago Catemaco, U.I.M.N.H. (1); 4 kilometers northeast of Minatitlán, T.N.H.C. (1); 2 kilometers south of Naranja, U.M.M.Z. (12); San Lorenzo, U.S.N.M. (3).

BRITISH HONDURAS: *Cayo*: 2 kilometers southwest of Cayo, U.M.M.Z. (5); Hummingbird Highway, 16 kilometers from Belize-Cayo road, U.M.M.Z. (6); Pine Ridge Road, 20.3 kilometers from Belize-Cayo road, U.M.M.Z. (2); Pine Ridge Road, 57-58 kilometers from Belize-Cayo road, U.M.M.Z. (1); San Augustine, U.M.M.Z. (1).

GUATEMALA: *Alta Verapaz*: Finca Chama, C.A.S. (1), U.M.M.Z. (85). El Petén: No specific locality, U.S.N.M. (1); La Libertad, F.M.N.H. (2), K.U. (17, 1 skeleton), M.C.Z. (2), U.I.M.N.H. (1), U.M.M.Z. (8), U.S.N.M. (1); Piedras Negras, F.M.N.H. (3), U.I.M.N.H. (1), U.S.N.M. (1); 8 kilometers south of Piedras Negras, U.S.N.M. (32); Tikal, U.M.M.Z. (3); Toocog, 15 kilometers southeast of La Libertad, K.U. (9, 5 skeletons, 1 eggs). *Isabal*: Puerto Barrios, F.M.N.H. (2); 8 kilometers south of Puerto Barrios, K.U. (9).

HONDURAS: *Francisco Morazan*: Cerro de Cuaimaca, U.M.M.Z. (1); Cerro Uyuca, A.M.N.H. (1), U.M.M.Z. (2). *Yoro*: Subirana Valley, F.M.N.H. (1), M.C.Z. (4).

NICARAGUA: *Boaco*: 14 kilometers north, 13 kilometers east of Boaco, K.U. (7). *Estelí*: Finca Daraili, 5 kilometers north, 14 kilometers east of Condega, K.U. (2); Finca Venecia, 7 kilometers east of Condega, K.U. (6). *Matagalpa*: 14.4 kilometers southeast of Jinotega, K.U. (1); 19 kilometers north of Matagalpa, U.M.M.Z. (10); Santa María de Ostuma, K.U. (1). *Zelaya*: Isla Grande del Maiz, K.U. (5).

COSTA RICA: *Cartago*: El Silencio, 14.4 kilometers northeast of Turrialba, K.U. (2); Moravia de Turrialba, K.U. (13, 1 skeleton, 1 tadpoles, 1 eggs), U.S.C. (25); 11 kilometers southwest of Moravia, K.U. (2); 1 kilometer east-northeast of Pacuare, K.U. (17); Peralta, K.U. (5); Tuis, K.U. (1); Turrialba, F.M.N.H. (12), K.U. (48, 3 skeletons), U.S.C. (9),

U.M.M.Z. (5). *Guanacaste*: Finca San Bosco, U.S.C. (21); Silencio, U.S.C. (14); Tilarán K.U. (8), 2 kilometers east of Tilarán, K.U. (27, 2 skeletons); 4 kilometers east of Tilarán, U.S.C. (4); 8 kilometers northeast of Tilarán, K.U. (15). *Heredia*: Finca La Selva, U.S.C. (3); Puerto Viejo, K.U. (3, 3 skeletons).

*Hyla melanomma bivocata*

MEXICO: *Chiapas*: 32 kilometers north of Jitotol, U.I.M.N.H. (3); 18 kilometers north of Pueblo Nuevo Solistahuacán, K.U. (1), U.M.M.Z. (4); 5.6 kilometers south of Rayón Mescalapa, K.U. (1, 1 skeleton); 6.2 kilometers south of Rayón Mescalapa, K.U. (5).

*Hyla melanomma melanomma*

MEXICO: *Guanacaste*: Acahuitzotla, T.C.W.C. (3); Agua del Obispo, A.M.N.H. (3), K.U. (1, 1 tadpoles); 11 kilometers east of Chilpancingo, F.M.N.H. (17), M.C.Z. (1), U.I.M.N.H. (10), U.M.M.Z. (1), U.S.N.M. (6); 22 kilometers south of Chilpancingo, C.A.S. (8). *Oaxaca*: 29 kilometers south-southeast of Juchatengo, K.U. (1); 56 kilometers north of Pochutla, U.M.M.Z. (1); 62 kilometers north of Pochutla, U.M.M.Z. (6); 6 kilometers north-northwest of San Cabriel Mixtepec, K.U. (1, 1 tadpoles); 12 kilometers north-northwest Mixtepec, K.U. (16, 2 skeletons).

*Hyla microcephala microcephala*

COSTA RICA: *Puntarenas*: Colfito, K.U. (36); 3 kilometers east of Colfito, K.U. (1), U.S.C. (2); Palmar Sur, K.U. (24, 5 skeletons), U.S.C. (14), U.U. (26); 3 kilometers northwest of Piedras Blancas, K.U. (11); Villa Neilly, U.S.C. (12); 10.5 kilometers west-northwest of Villa Neilly, K.U. (19, 1 eggs).

PANAMA: *Canal Zone*: Albrook Air Base, T.N.H.C. (2); Balboa, A.N.S.P. (2); Fort Clayton, U.I.M.N.H. (5); 2.8 kilometers southwest of Fort Kobbe, K.U. (11); Frijoles, M.C.Z. (1); Camboa M.C.Z. (1); 8.3 kilometers north of Catún Locks, T.N.H.C. (1); Juan Díaz, M.C.Z. (1); Juan Mina, A.M.N.H. (2), A.N.S.P. (2), U.M.M.Z. (7), U.U. (7); Madden Dam, F.M.N.H. (1); 8-14 kilometers north of Miraflores Locks, T.N.H.C. (116); Río Chagres, A.M.N.H. (2); Río Cocolí, 3.5 kilometers north of Miraflores Locks, T.N.H.C. (1); Summit, A.N.S.P. (7), F.M.N.H. (4), K.U. (5). *Chiriquí*: 5.5 kilometers east of Concepción, A.M.N.H. (1); 14.4 kilometers east of Concepción, A.M.N.H. (6); 2 kilometers south of David (1); Progreso, U.M.M.Z. (5); Río Cariché, 8.3 kilometers east-southeast of Paso Canoas, K.U. (4). *Cocle*: 1 kilometer southeast of El Caño, K.U. (10); El Valle de Antón, A.M.N.H. (11), A.N.S.P. (4), K.U. (14), M.V.Z. (6), U.I.M.N.H. (1). *Colón*: Cement Plant, Transisthmian Highway, F.M.N.H. (1). *Darién*: El Real, K.U. (15), U.M.M.Z. (10), U.S.N.M. (2); Río Canclon at Río Chucunaque, U.M.M.Z. (1); Río Chucunaque, near Yavisa, A.M.N.H. (1). *Los Santos*: Tonosí: K.U. (4). *Panamá*: 5 kilometers south of Bejuco, A.M.N.H. (1);

3 kilometers west of Chepo, K.U. (3, 2 tadpoles); 6 kilometers west-southwest of Chepo, K.U. (1); Chico, Río La Jagua, U.S.N.M. (1); La Joya, A.M.N.H. (5); Nueva Gorgona, A.M.N.H. (2); 1.6 kilometers west of Nueva Gorgona, A.M.N.H. (1); 9 kilometers northeast of Pacora, K.U. (1); 1.5 kilometers west of Pacora, K.U. (25); Panamá, K.U. (1); Río La Laja, near Chamé, A.N.S.P. (1); Río Tapia, A.M.N.H. (4); 18 kilometers east of Tucunén, M.V.Z. (1). *Vera-guas*: Río Coroba, U.S.N.M. (1).

*Hyla m. microcephala* x *underwoodi*

COSTA RICA: *Puntarenas*: Parrita, U.S.C. (9); 6.1 kilometers northeast of mouth of Río Tarcoles, U.S.C. (4).

*Hyla microcephala underwoodi*

MEXICO: *Campeche*: Balchacaj, F.M.N.H. (1), U.I.M.N.H. (3); Encarnación, F.M.N.H. (3), M.C.Z. (2), U.I.M.N.H. (12), U.S.N.M. (2); Escárcega, U.M.M.Z. (1); 7.5 kilometers west of Escárcega, K.U. (15); Laguna Alvarado, 65 kilometers south of Xpujil, K.U. (6); Pacaitún, Río Candelaria, F.M.N.H. (3); Tres Brazos, F.M.N.H. (22), U.I.M.N.H. (1); 10 kilometers west of Xpujil, K.U. (2). *Chiapas*: Palenque, U.I.M.N.H. (13), U.S.N.M. (6). *Oaxaca*: 5 kilometers north of Chiltepec, K.U. (9); 3 kilometers north of Donají, U.M.M.Z. (14); 43 kilometers north of Matías Romero, U.I.M.N.H. (19); 3.5 kilometers north of Palomares, T.N.H.C. (40); 4.6 kilometers north of Sarabia, U.M.M.Z. (2); 6.1 kilometers north of Sarabia, U.M.M.Z. (11); 3 kilometers north of Toluca, K.U. (1); Tuxtepec, K.U. (17); 3 kilometers south of Tuxtepec, U.I.M.N.H. (100). *Tabasco*: 24 kilometers north of Frontera, M.C.Z. (6), U.I.M.N.H. (4); 0.8 kilometers east of the Río Tonalá, T.N.H.C. (1); Teapa, U.M.M.Z. (4); 2.7 kilometers north of Teapa, U.M.M.Z. (4); 10 kilometers north of Teapa, U.M.M.Z. (6); 11.5 kilometers north of Teapa, U.M.M.Z. (1); 15.2 kilometers north of Teapa, U.M.M.Z. (4); 17.6 kilometers north of Teapa, U.M.M.Z. (12); 3.3 kilometers south of Villahermosa, U.M.M.Z. (12); 17.6 kilometers south of Villahermosa, U.M.M.Z. (12). *Veraeruz*: 2.1 kilometers north of Acajucan, U.I.M.N.H. (3); 6.4 kilometers northwest of Acajucan, U.M.M.Z. (14); 1.6 kilometers east-southeast of Alvarado, U.M.M.Z. (39); 2.4 kilometers east-southeast of Alvarado, U.M.M.Z. (2); 4.5 kilometers south of Aquilera, U.M.M.Z. (21); 8 kilometers southwest of Coatzacoaleos, U.M.M.Z. (10); 13 kilometers north of Corral Nuevo, U.I.M.N.H. (7); 2.2 kilometers east of Cosaleaque, U.M.M.Z. (26); 10 kilometers southeast of Hueyapan, U.M.M.Z. (1); 0.8 kilometer south of Lerdo de Tejada, U.M.M.Z. (1); 3.6 kilometers northeast of Minatitlán, T.N.H.C. (3); 1.9 kilometers south of Naranja, U.M.M.Z. (3); 4.5 kilometers northeast of Novillero, U.M.M.Z. (1); San Andrés Tuxtla, F.M.N.H. (5), U.I.M.N.H. (2). *Yucatán*: Chichén-Itzá, F.M.N.H. (1), M.C.Z. (2).

BRITISH HONDURAS: *Cayo*: 6.2 kilometers south of El Cayo, M.C.Z. (8). *Stann Creek*: Stann Creek, F.M.N.H. (1).

GUATEMALA: *Alta Verapaz*: 28.3 kilometers north of Campur, K.U. (13); Chinajá, K.U. (1); Cubilquitz, U.M.M.Z. (5); Finca Chamá, U.M.M.Z. (163); Finca Tinaja, B.Y.U. (1); Panzós, U.M.M.Z. (2). *Chiquimula*: Chiquimula, U.M.M.Z. (1); 2 kilometers north of Esquipulas, U.M.M.Z. (1). *El Petén*: La Libertad, K.U. (51, 5 skeletons), M.C.Z. (1), U.M.M.Z. (48); Piedras Negras, F.M.N.H. (1), U.I.M.N.H. (1); 5 kilometers south of Piedras Negras, U.S.N.M. (22); Tikal, U.M.M.Z. (2); Toocog, 15 kilometers southeast of La Libertad, K.U. (21). *El Quiché*: Finca Tesoro, U.M.M.Z. (5). *Huehuetenango*: Finca San Rafael, 16 kilometers southeast of Barillas, F.M.N.H. (3). *Izabal*: Murciélago, Lago Izabal, U.I.M.N.H. (5); Puerto Barrios, F.M.N.H. (4); 8 kilometers south of Puerto Barrios, K.U. (31, 1 eggs, 1 tadpoles); Quirigua, C.A.S. (45); 2.5 kilometers northeast of Río Blanco, K.U. (1); San Felipe, F.M.N.H. (1). *Zacapa*: 14 kilometers east-northeast of Mayuelas, K.U. (5); 8 kilometers east-northeast of Río Hondo, K.U. (4).

HONDURAS: *Atlántida*: La Ceiba, U.M.M.Z. (2), U.S.N.M. (8); Lancetilla, M.C.Z. (1). *Cortes*: Lago Yojoa, A.M.N.H. (5), K.U. (15). *El Paraíso*: Valle de Jamastrán, A.M.N.H. (6). *Francisco-Morazán*: El Zamorano, A.M.N.H. (9), K.U. (1), U.M.M.Z. (1); Montaña de Cuaimaea, A.M.N.H. (8); Rancho San Diego, 19 kilometers southwest of Guaimaea, A.M.N.H. (1). *Itibucá*: Vieja Itibucá, A.M.N.H. (2).

NICARAGUA: *Boaco*: 14 kilometers north, 13 kilometers east of Boaco, K.U. (19). *Chontales*: 11.7 kilometers east of Santo Tomás, K.U. (1); 3 kilometers southwest of Santo Tomás, K.U. (10, 1 skeleton). *Esteli*: Finca Venecia, 7 kilometers north, 16 kilometers east of Condega, K.U. (1); 2.4 kilometers north of Esteli, M.C.Z. (5). *Managua*: 12-13 kilometers east of Managua, K.U. (5); 10 kilometers southwest of Tipitapa, U.M.M.Z. (10). *Matagalpa*: Finca Tepeyac, 10.5 kilometers north, 9 kilometers east of Matagalpa, K.U. (2); Hacienda La Cumplida, K.U. (17, 3 skeletons), U.M.M.Z. (42); 14.4 kilometers southeast of Jinotega, K.U. (1). *Nueva Segovia*: 5 kilometers north, 2.5 kilometers east of Jalapa, K.U. (38). *Rivas*: Finca Amayo, 13 kilometers south, 14 kilometers east of Rivas, K.U. (4); 16 kilometers south of Rivas, M.C.Z. (7); 20.5 kilometers southeast of Rivas, K.U. (3); 5 kilometers southeast of San Pablo, K.U. (4). *Zelaya*: El Recreo, K.U. (1).

COSTA RICA: *Guanacaste*: Arenal, U.S.C. (2); 3 kilometers west of Bagaces, U.S.C. (10); Finca San Bosco, U.S.C. (9); Guayabo de Bagaces, U.S.C. (8); 12 kilometers south of La Cruz, U.S.C. (2); Laguna Arenal, U.S.C. (1); 27 kilometers north of Las Cañas, U.S.C. (6); 16 kilometers east of Las Cañas, K.U. (7); 16 kilometers south-southeast of Las Cañas, K.U. (6); 20 kilometers southeast of Las Cañas, K.U. (1); Liberia, U.S.C. (9); 7.3 kilometers north of Liberia, U.S.C. (4); 10 kilometers north of Liberia, U.S.C. (9); 7.5 kilometers southeast of Liberia, K.U. (7, 2 skeletons); 14.7 kilometers south of Liberia, U.S.C.



(3); 4 kilometers west of Liberia, K.U. (11); 2 kilometers south of Nicoya, U.S.C. (1); 3-10 kilometers east-southeast of Playa del Coco, U.S.C. (30); 21.6 kilometers east-southeast of Playa del Coco, U.S.C. (13); Peñas Blancas, K.U. (4); Río Bebedero, 5 kilometers south of Bebedero, K.U. (1); Río Higuerón, U.S.C. (2); Santa Cruz, U.S.C. (2); Silencio, U.S.C. (1); Tenorio, K.U. (1); Tilarán, K.U. (3), 2 kilometers east of Tilarán, K.U. (1); 5 kilometers northeast of Tilarán, K.U. (7), U.S.C. (1). *Puntarenas*: Barranca, K.U. (8); 5 kilometers west-northwest of Barranca, U.M.M.Z. (2); 3 kilometers northeast of Boca del Barranca, U.S.C. (21); 10 kilometers east of Esparta, K.U. (3, 1 tadpoles); 1 kilometer west-northwest of Esparta, K.U. (1); 4 kilometers west-northwest of Esparta, K.U. (1); 10 kilometers west-northwest of Esparta, K.U. (25, 5 skeletons); 12 kilometers west-northwest of Esparta, K.U. (5), U.S.C. (1); 21.8 kilometers west of San Ramón U.S.C. (15).

#### *Hyla miliaria*

NICARAGUA: No specific locality, U.S.N.M. (1).

COSTA RICA: *Cartago*: Turrialba, K.U. (1).

PANAMA: *Chiriquí*: Finca Santa Clara, K.U. (2). *Coclé*: El Valle, A.M.N.H. (1).

#### *Hyla miotympanum*

MEXICO: *Chiapas*: No specific locality, U.S.N.M. (1); 16.5 kilometers north of Pueblo Nuevo Solistahuacán, U.M.M.Z. (15). *Guerrero*: ?Acapulco, F.M.N.H. (1), U.I.M.N.H. (1). *Hidalgo*: 9.4 kilometers north of Metzquititlán, K.U. (20, 1 tadpoles); Río Chinameca, 7.2 kilometers north of Tianguistengo, K.U. (2, 4 tadpoles); Tianguistengo, C.A.S. (1), F.M.N.H. (19), U.I.M.N.H. (9). 3 kilometers southeast of Xochicoatlán, K.U. (5, 1 tadpoles); Zacualtípán, A.N.S.P. (1); 8.5 kilometers southeast of Zacualtípán, K.U. (1); 6 kilometers south of Zacualtípán, F.M.N.H. (12), U.I.M.N.H. (5). *Nuevo León*: Hacienda Pablillo, above Galeana, A.N.S.P. (1); Parajé de los Osos, Villa de Santiago, K.U. (19); Salto Cola de Caballo, A.M.N.H. (2), A.N.S.P. (1), I.P.N. (6), K.U. (9), M.V.Z. (1), T.N.H.C. (20), U.I.M.N.H. (9), U.M.M.Z. (15); Santiago, Vista Hermosa, F.M.N.H. (10); Zaragoza, K.U. (5). *Oaxaca*: Cerro San Felipe, F.M.N.H. (1), U.I.M.N.H. (1); ?Tehuantepec, U.S.N.M. (3). *Puebla*: 4.5 kilometers northeast of Huachinango, U.M.M.Z. (1); 14.4 kilometers west of Huachinango, K.U. (71, 4 skeletons), U.M.M.Z. (19, 1 skeleton, 1 tadpoles); 15.6 kilometers west of Huachinango, K.U. (1); 16 kilometers west of Huachinango, A.M.N.H. (2); ?Izúcar de Matamoros, Z.M.B. (2); Lago Necaxa, U.M.M.Z. (1); Río Frio, 10.7 kilometers north-northeast of Tezuitlán, K.U. (1, 1 tadpoles); Río Octapa, 3.7 kilometers north-northeast of Tezuitlán, K.U. (36, 1 tadpoles); Río San Marcos, U.M.M.Z. (1); Río Texcapa, 5 kilometers east of Huachinango, K.U. (3); San Diego de Tehuacán, U.M.M.Z. (14), U.S.N.M.

(4). *San Luis Potosí*: 8 kilometers west of La Meca, T.C.W.C. (2); Naranjo, F.M.N.H. (8), U.I.M.N.H. (4); Palictla, A.M.N.H. (3), M.C.Z. (18); Patilla, 8 kilometers north of Tamazunchale, U.M.M.Z. (2); Tamazunchale, U.I.M.N.H. (1), U.M.M.Z. (11); 3 kilometers north of Tamazunchale, T.C.W.C. (1), U.I.M.N.H. (1); 5 kilometers north of Tamazunchale, T.C.W.C. (2); 12.4 kilometers north of Tamazunchale, T.N.H.C. (5); 50 kilometers south of Valles, F.M.N.H. (9), U.I.M.N.H. (4); Xilitla, A.M.N.H. (1), K.U. (1), U.S.N.M. (1 tadpoles); 1.6 kilometers northwest of Xilitla, U.I.M.N.H. (1, 1 tadpoles). *Tamaulipas*: Acuña, U.M.M.Z. (1 tadpoles); 5 kilometers northwest of Acuña, U.M.M.Z. (16); 2 kilometers southeast of La Joya de Salas, U.M.M.Z. (22); Las Yucas, north of Aldama, M.C.Z. (5); 5 kilometers northwest of San José, U.M.M.Z. (1); Santa Barbara, U.M.M.Z. (2); 1.6 kilometers north of Santa Inéz, U.I.M.N.H. (2). *Veracruz*: Acultzingo, U.I.M.N.H. (2), U.M.M.Z. (3), U.S.N.M. (1); 8 kilometers east of Acultzingo, U.S.N.M. (15); 2 kilometers west of Acultzingo, U.I.M.N.H. (5), U.S.N.M. (15); Arroyo del Meco, near Linales, M.C.Z. (2); Banderilla, F.M.N.H. (7), U.I.M.N.H. (4); Barranca Metlac, F.M.N.H. (38), M.C.Z. (41), K.U. (1, 11 skeletons, 1 tadpoles, 1 eggs); U.I.M.N.H. (60), U.M.M.Z. (211, 2 tadpoles); Córdoba, F.M.N.H. (5), U.S.N.M. (2); Coscomatepec, K.U. (43); 5.5 kilometers north-northeast of Coscomatepec, U.M.M.Z. (3); 4.3 kilometers west of Coscomatepec, U.M.M.Z. (1); 7 kilometers west of Coscomatepec, U.M.M.Z. (1); Cuautlapan, F.M.N.H. (3), K.U. (32), U.I.M.N.H. (54), U.S.N.M. (15). Cumbres de Acultzingo, F.M.N.H. (11), M.C.Z. (2), U.I.M.N.H. (8), U.M.M.Z. (3); Fortín de las Flores, U.I.M.N.H. (1), U.M.M.Z. (5); 1.6 kilometers north of Fortín de las Flores, U.I.M.N.H. (56); 3 kilometers north of Fortín de las Flores, U.I.M.N.H. (1); 9 kilometers southwest of Fortín de las Flores, U.M.M.Z. (2); 5 kilometers west of Fortín de las Flores, U.I.M.N.H. (9), U.S.N.M. (15). Huatusco, K.U. (6). 7 kilometers northeast of Huatusco, U.M.M.Z. (18); 1.6 kilometers south of Huatusco, U.I.M.N.H. (1); 3 kilometers southwest of Huatusco, K.U. (5 skeletons), U.M.M.Z. (57); 7.5 kilometers southwest of Huatusco, U.M.M.Z. (9); 12 kilometers southwest of Huatusco, U.M.M.Z. (1); Jalapa, B.M.N.H. (5), F.M.N.H. (14), U.I.M.N.H. (8); 5 kilometers north of Jalapa, K.U. (11), T.C.W.C. (1); 10 kilometers south of Jalapa, U.M.M.Z. (1); La Perla, M.C.Z. (93), U.I.M.N.H. (21); Laguna Encatada, Sierra de los Tuxtlas, U.M.M.Z. (8); Los Chaneques, 2 kilometers north of Santiago, Tuxtla, U.I.M.N.H. (3), U.M.M.Z. (22, 1 tadpoles); Mirador, U.S.N.M. (2); Orizaba, M.C.Z. (5), U.M.M.Z. (13); 2 kilometers north of Parajé Nuevo, K.U. (1); Potrero, F.M.N.H. (1), U.I.M.N.H. (4), U.S.N.M. (3), U.M.M.Z. (1); Potrero Viejo, U.M.M.Z. (1); Río Sordo, 3 kilometers west of Jalapa, F.M.N.H. (5); 3 kilometers north-northeast of San Andrés Tuxtla, T.C.W.C. (3), U.M.M.Z. (5, 1 tadpoles); 6 kilometers southeast of Tebanca, T.C.W.C. (1); between Tebanca and Volcán Santa María, U.M.M.Z. (1); Tequayutepec, M.C.Z.

(3); Teocelo, K.U. (18); 3 kilometers north of Teocelo, F.M.N.H. (3); 15 kilometers east-northeast of Tlacotepec, K.U. (1); 4 kilometers west of Tlapacoyán, K.U. (1); Volcán Pajapan, U.I.M.N.H. (3); southeast slope of Volcán San Martín, K.U. (45, 3 skeletons, 2 tadpoles, 2 eggs), U.I.M.N.H. (19), U.M.M.Z. (10); Xico, U.I.M.N.H. (21), U.S.N.M. (1); between Xometla and La Perla, Pico de Orizaba, K.U. (14); Zongolica, I.P.N. (1).

#### *Hyla mixe*

MEXICO: *Oaxaca*: 4.2 kilometers south of Campamento Vista Hermosa, K.U. (2, 1 skull, 1 tadpoles).

#### *Hyla mixomaculata*

MEXICO: *Veracruz*: Barranca metlac, U.M.M.Z. (2); Coscomatepec, K.U. (7, 2 skeletons); 7.2 kilometers southwest of Coscomatepec, U.M.M.Z. (1); Huatusco, K.U. (2); 3 kilometers southwest of Huatusco, K.U. (1 tadpoles), U.M.M.Z. (1 tadpoles); 7.5 kilometers southwest of Huatusco, U.M.M.Z. (1); 12 kilometers southwest of Huatusco, U.M.M.Z. (2); Sumidero, M.C.Z. (1); 1.6 kilometers west of Xico, U.M.M.Z. (3).

#### *Hyla nubicola*

MEXICO: *Veracruz*: Barranca Metlac, U.M.M.Z. (1, 1 skeleton); 7 kilometers northeast of Huatusco, U.M.M.Z. (1); 1.9 kilometers south of Huatusco, U.I.M.N.H. (1); 3 kilometers southwest of Huatusco, K.U. (1), U.M.M.Z. (1).

#### *Hyla pachyderma*

MEXICO: *Veracruz*: Pan de Olla, south of Tezuatlán, Veracruz, U.S.N.M. (4).

#### *Hyla pellita*

MEXICO: *Oaxaca*: 30 kilometers north of San Cabriel Mixtepec, K.U. (2); 33 kilometers north of San Cabriel Mixtepec, K.U. (3, 1 skeleton).

#### *Hyla penthetec*

MEXICO: *Oaxaca*: 29 kilometers south-southeast of Juchatengo, K.U. (1); Pluma Hidalgo, A.M.N.H. (1); 37 kilometers north of San Cabriel Mixtepec, K.U. (3, 1 skeleton, 1 tadpoles), U.M.M.Z. (5).

#### *Hyla phlebodes*

NICARAGUA: *Zelaya*: Isla Grande del Maíz, M.C.Z. (1); Río Mico, Recrero, K.U. (1), U.M.M.Z. (6).

COSTA RICA: *Alajuela*: 12.4 kilometers north of Florencia, M.V.Z. (3), U.S.C. (1); Las Playuelas, 11 kilometers south of Los Chiles, U.S.C. (1); Los Chiles, U.S.C. (2); 3 kilometers northeast of Muelle de Arenal, U.S.C. (2); "San Carlos," U.S.N.M. (1).

*Cartago*: Chitaria, K.U. (1); El Silencio, 14.4 kilometers northeast of Turrialba, K.U. (2); 1.6 kilometers east of the Río Reventazón bridge, east of Turrialba, U.M.M.Z. (2); Tunnel camp, near Peralta, K.U. (13, 1 skeleton); Turrialba, F.M.N.H. (3), K.U. (46, 6 skeletons, 1 eggs, 1 tadpoles), M.C.Z. (5), U.M.M.Z. (10), U.S.C. (16), U.S.N.M. (1). *Guanaacaste*: Arenal, U.S.C. (1); Finca San Bosco, U.S.C. (7); Guayabo de Bagaces, U.S.C. (4); Laguna Arenal, U.S.C. (4); 3 kilometers northeast of Tilarán, U.S.C. (1); 6 kilometers northeast of Tilarán, U.M.M.Z. (6, 1 skeleton), U.S.C. (9). *Heredia*: Puerto Viejo, K.U. (46, 5 skeletons, 4 tadpoles); 4.2 kilometers west of Puerto Viejo, K.U. (2); 5.9 kilometers west of Puerto Viejo, K.U. (5); 7.5 kilometers west of Puerto Viejo, K.U. (1). *Limón*: Batán, U.M.M.Z. (2); La Castilla, A.N.S.P. (1); Puerto Limón, K.U. (7).

PANAMA: *Bocas del Toro*: 3.2 kilometers northwest of Almirante, K.U. (1); Cayo de Agua, K.U. (5); Fish Creek, K.U. (3); Isla Escudo de Veraguas, K.U. (2); mouth of Río Cahuita, K.U. (2). *Canal Zone*: Barro Colorado Island, A.M.N.H. (1), A.N.S.P. (7), F.M.N.H. (4); Juan Mina, A.M.N.H. (1), U.U. (1); 8.6-13.8 kilometers north of Miraflores Locks, T.N.H.C. (63); Río Chagres, A.M.N.H. (4); Río Cocolí, 3.5 kilometers north of Miraflores Locks, T.N.H.C. (11); Summit, A.N.S.P. (1); Three Rivers Plantation, S.U. (1). *Coclé*: El Valle de Antón, A.M.N.H. (5), A.N.S.P. (4). *Colón*: Achioté, K.U. (64); Ciricito, C.A.S. (4). *Darién*: Río Canclon at Río Chucunaque, U.M.M.Z. (1); Río Chucunaque, near Yavisa, A.M.N.H. (1). *Panamá*: Cerro La Campana, F.M.N.H. (4) *San Blas*: Sasardi, K.U. (1). *Veraguas*: mouth of Río Concepción, K.U. (1).

#### *Hyla picadoi*

COSTA RICA: *Alajuela*: Poasito, U.F. (1); 13 kilometers northwest of Poasito, U.S.C. (1); Río Poasito, 1 kilometer west of Poasito, K.U. (2, 1 skeleton). *Cartago*: 1 kilometer southeast of La Chonta, U.S.C. (1); 6 kilometers north of Las Cruces, (6); Volcán Turrialba, U.M.M.Z. (1). *Heredia*: Volcán Barba, A.N.S.P. (3), M.C.Z. (1), U.M.M.Z. (1). *San José*: El Empalme, K.U. (1), U.S.C. (1).

PANAMA: *Bocas del Toro*: north slope Cerro Pando, 1920 meters, K.U. (2).

#### *Hyla picta*

MEXICO: *Campeche*: 7.5 kilometers west of Escárcega, K.U. (16); Matamoros, F.M.N.H. (11); Paicatún Río Candelaria, F.M.N.H. (27); Tres Brazos, F.M.N.H. (1). *Chiapas*: Palenque, U.I.M.N.H. (3); 18 kilometers south of Teapa (Tabasco), U.I.M.N.H. (1). *Oaxaca*: 5 kilometers north of Chiltepec, K.U. (3); 3 kilometers north of Donaji, U.M.M.Z. (8); 78 kilometers north of La Venta, T.N.H.C. (4); 85 kilometers north of La Venta, T.N.H.C. (1); 3.7 kilometers north of Sarabia, U.M.M.Z. (11); 1.6 kilometers south of Tolosita, U.M.M.Z. (14); Tuxtepec, K.U. (2), U.I.M.N.H. (14); 3 kilometers south of Tux-

tepec, U.I.M.N.H. (1) 13 kilometers south of Tuxtepec, U.I.M.N.H. (3); 1 kilometer south of Uvero, U.M.M.Z. (6); 2 kilometers south of Valle Nacional, K.U. (1). *Puebla*: 9 kilometers south of Tepeojuma, U.M.M.Z. (5); San Diego, A.M.N.H. (15); Villa Juárez, T.N.H.C. (18), U.I.M.N.H. (4). *San Luis Potosí*: 16 kilometers north of Tamazunchale, U.I.M.N.H. (3); Valles, F.M.N.H. (2). *Tabasco*: Frontera, U.S.N.M. (8); 6 kilometers west of Palo Mulato, U.M.M.Z. (3); Teapa, U.M.M.Z. (34); 10 kilometers north of Teapa, U.M.M.Z. (4); 15 kilometers north of Teapa, U.M.M.Z. (1); Villahermosa, U.I.M.N.H. (2); 17 kilometers south of Villahermosa, U.M.M.Z. (3). *Veracruz*: 19 kilometers north of Acayucan, U.I.M.N.H. (4); 2.5 kilometers east-southeast of Alvarado, U.M.M.Z. (5); 3.2 kilometers southeast of Alvarado, U.M.M.Z. (5); 4.5 kilometers south of Aquilera, U.M.M.Z. (1); Barranca Metlac, U.I.M.N.H. (6); 10 kilometers south of Catemaco, U.M.M.Z. (2); 8 kilometers southwest of Coatzacoalcas, U.M.M.Z. (1); 5 kilometers east-southeast of Córdoba, T.N.H.C. (39); 6.4 kilometers east-southeast of Córdoba, A.M.N.H. (16), U.M.M.Z. (14); Coyame, U.I.M.N.H. (1), U.M.M.Z. (6); Cuautlapan, F.M.N.H. (1), U.I.M.N.H. (9), U.S.N.M. (6); 1.6 kilometers east-northeast of Encinal, U.M.M.Z. (2); 1 kilometer south of Encinal, U.M.M.Z. (4); Hacienda Tamiahua, Cabo Rojo, K.U. (1); 3 kilometers southwest of Huatusco, U.M.M.Z. (60); 10 kilometers southeast of Hueyapan, U.M.M.Z. (7); 20 kilometers east-northeast of Jesús Carranza, K.U. (1); north side Lago de Catemaco, K.U. (3); 21.6 kilometers south of Las Choapas, T.C.W.C. (4); 5 kilometers northwest of Lerdo de Tejada, U.M.M.Z. (1); 17 kilometers east of Martínez del Torre, U.I.M.N.H. (1); 6.4 kilometers west of Martínez del Torre, U.I.M.N.H. (2); 2 kilometers east-northeast of Mata Oscura, K.U. (19); 4 kilometers northeast of Miniatitlán, T.N.H.C. (1); Orizaba, U.S.N.M. (1); Potrero Viejo, F.M.N.H. (5), M.C.Z. (2), U.I.M.N.H. (56), U.M.M.Z. (68), U.S.N.M. (25); Tierra Colorada, F.M.N.H. (6), U.I.M.N.H. (3); Tlalpan, F.M.N.H. (2); 2.7 kilometers northwest of Tula, U.M.M.Z. (3); 8 kilometers south of Veracruz, U.M.M.Z. (2); 3 kilometers west of Veracruz, U.I.M.N.H. (15); 7 kilometers west of Veracruz, K.U. (1).

BRITISH HONDURAS: *Cayo*: 5 kilometers southwest of Cayo, U.M.M.Z. (6); 6.4 kilometers south of Cayo, M.C.Z. (3); 5 kilometers west of Pine Ridge road on Belize-Cayo highway, U.M.M.Z. (1). *Stann Creek*: 10 kilometers east of Stann Creek, U.M.M.Z. (1).

GUATEMALA: *Alta Verapaz*: 5.1 kilometers northeast of Campur, K.U. (6); Finca Chama, U.M.M.Z. (72); 13 kilometers south of Sebol, T.N.H.C. (1). *El Petén*: Dolores, U.M.M.Z. (1); La Libertad, U.M.M.Z. (7); Toocog, 15 kilometers southeast of La Libertad, K.U. (8). *Izabal*: Puerto Barrios, T.C.W.C. (5); 2.5 kilometers northeast of Río Blanco, K.U. (12, 2 skeletons).

HONDURAS: *Atlántida*: Ceiba, U.S.N.M. (1); Lancetilla, M.C.Z. (6).

### *Hyla pictipes*

COSTA RICA: *Alajuela*: Río Poasito, 1 kilometer north of Poasito, K.U. (68, 4 skeletons, 4 tadpoles), M.C.Z. (2); Volcán Poás, U.M.M.Z. (1 tadpoles). *Cartago*: 0.5 kilometers east of Tierra Blanca, U.M.M.Z. (1 tadpoles). *Heredia*: Paso Llano, south slope of Volcán Barba, K.U. (13 tadpoles); Rama Sur of Río Las Vueltas, south slope of Volcán Barba, K.U. (7, 1 skeleton), U.S.C. (29); Volcán Barba, U.S.C. (6). *San José*: south slope of Cerro de la Muerte, U.S.C. (4); La Palma, A.N.S.P. (8), U.M.M.Z. (1); 2 kilometers north of Las Nubes, K.U. (1); 3 kilometers southeast of Rancho Redondo, U.M.M.Z. (2), U.S.C. (2).

### *Hyla pinorum*

MEXICO: *Guerrero*: Agua del Obispo, F.M.N.H. (1), K.U. (1 tadpoles), U.I.M.N.H. (1); 1.6 kilometers east of San Andreas de la Cruz, K.U. (3, 1 tadpoles), U.M.M.Z. (3, 1 skeleton, 1 tadpoles); 3.3 kilometers north of San Vicente, K.U. (5). *Oaxaca*: San Vicente, U.I.M.N.H. (1).

### *Hyla plicata*

MEXICO: No specific locality, M.N.H.N. (1). *Distrito Federal*: Cañon Contreras, 10 kilometers southwest of Ciudad México, U.M.M.Z. (2); Desierto de los Leones, A.M.N.H. (4, 1 tadpoles), M.C.Z. (1); Pico Santo Rosa, U.M.M.Z. (1); 15.5 kilometers southwest of Villa Obregón, U.M.M.Z. (1). *Hidalgo*: El Chico Parque Nacional, A.M.N.H. (5), K.U. (21, 1 skeleton, 1 tadpoles), U.I.M.N.H. (5), U.S.N.M. (3); Guerrero, M.C.Z. (3), U.M.M.Z. (2); San Miguel Regla, F.M.N.H. (2), U.M.M.Z. (4); Velasco, A.M.N.H. (12), M.C.Z. (1). *México*: 23 kilometers west of Ciudad México, M.V.Z. (1); 55 kilometers southeast of Ciudad México, T.C.W.C. (9); 5 kilometers west of Las Cruces, U.I.M.N.H. (2); Llano Grande near Río Frío, F.M.N.H. (1), M.C.Z. (2), T.C.W.C. (21), U.I.M.N.H. (28), U.S.N.M. (23); Nevado de Toluca, A.M.N.H. (1), F.M.N.H. (1); Salazar, I.P.N. (2); San Juan Teotihuacán, A.M.N.H. (2), M.C.Z. (2); 5.6 kilometers south of Tenango, T.C.W.C. (10); 18 kilometers north of Tenancingo, K.U. (1); Tlamacas, I.P.N. (1). *Michoacán*: Cerro San Andrés, U.M.M.Z. (26); 8 kilometers south-southeast of Opopeo, K.U. (4); 12 kilometers south-southeast of Opopeo, U.M.M.Z. (4); 3 kilometers east of San Gregorio, K.U. (56, 1 skeleton). *Morelos*: 3 kilometers west of Huitzilac, T.C.W.C. (5); 5 kilometers west of Huitzilac, U.M.M.Z. (1); 6 kilometers west of Huitzilac, K.U. (1); Lagunas de Zempoala, A.M.N.H. (8), F.M.N.H. (11), I.P.N. (11), T.C.W.C. (21), U.I.M.N.H. (58), U.S.N.M. (3); 7.3 kilometers southeast of Santa Martha, U.I.M.N.H. (2). *Puebla*: 14.4 kilometers northeast of Acatzingo, K.U. (1); Cruz Alto, south of Aquixtla, U.M.M.Z. (2); Río Otlati, 15 kilometers northwest of San Martín, T.C.W.C. (1). *Tlaxcala*: 5 kilometers northwest of Sanctorium, T.N.H.C. (1); 13 kilometers northeast of Tlaxcala, T.C.W.C. (1). *Veracruz*: 12 kilometers



southwest of Huatusco, U.M.M.Z. (2); Las Vigas, F.M.N.H. (2), U.I.M.N.H. (1), U.M.M.Z. (2).

#### *Hyla pseudopuma infucata*

PANAMA: *Bocas del Toro*: Río Claro near junction with Río Changena, K.U. (31, 5 skeletons); Río Changena, 830 meters, K.U. (11, 1 skeleton), M.C.Z. (2).

#### *Hyla pseudopuma pseudopuma*

COSTA RICA: *Alajuela*: 25 kilometers northwest of Barba U.M.M.Z. (2); Chinchona, K.U. (8, 1 skeleton, 4 tadpoles), U.S.C. (2); between Chinchona and Salto El Angel, U.S.C. (1); Salto El Angel, U.S.C. (1); 21 kilometers north of Varablanca, U.M.M.Z. (1); Volcán, Poás, K.U. (9), U.M.M.Z. (1 tadpoles); 1.6 kilometers south of Zapote, U.S.C. (2). *Cartago*: 29 kilometers south of Zapote, U.S.C. (1); 1 kilometer southeast of La Chonta, U.S.C. (3); Moravia de Turrialba, K.U. (15, 7 skeletons); Río Playas, U.S.C. (2); Tapantí, K.U. (52, 7 skeletons, 15 tadpoles, 1 eggs); Tuis, K.U. (1). *Heredia*: Finca El Conde de Tattenbach, south slope of Volcán Barba K.U. (4); Hacienda Cayuga, 1 kilometer north of Montaña Azul, K.U. (1); Isla Bonita, F.M.N.H. (1), K.U. (1); 9 kilometers north of La Concordia, K.U. (2); Montaña Azul, K.U. (1); 3 kilometers north of Montaña Azul, K.U. (1); Paso Llano, south slope of Volcán Barba, K.U. (3); Rama Sur of Río Las Vueltas, south slope of Volcán Barba, K.U. (16, 1 skeleton, 5 tadpoles), U.S.C. (1); Varablanca, K.U. (12); Volcán Barba, M.C.Z. (5), U.M.M.Z. (1 tadpoles), U.S.C. (1). *Puntarenas*: Monteverde, U.S.C. (19); 3.6 kilometers east of Monteverde, U.S.C. (14). *San José*: El Copey, M.C.Z. (1); El Empalme, U.S.C. (64), K.U. (1 tadpole); 3 kilometers northwest of El Empalme, K.U. (1); 7 kilometers southeast of El Empalme, K.U. (1); La Estrella, M.C.Z. (3); La Palma, A.N.S.P. (26), F.M.N.H. (3), K.U. (29, 3 tadpoles), M.C.Z. (2), U.M.M.Z. (10), U.S.C. (58), U.S.N.M. (1); Río Claro at Río La Hondura, U.S.C. (7); San Pedro, A.M.N.H. (3), U.S.C. (3); San Isidro, A.N.S.P. (2); 6.4 kilometers north of San Isidro el General, M.C.Z. (5); 14 kilometers north of San Isidro el General, K.U. (1); 15 kilometers north of San Isidro el General, K.U. (6, 6 tadpoles); 18 kilometers north of San Isidro el General, K.U. (1), U.M.M.Z. (1); 12.4 kilometers southwest of San Isidro el General, U.S.C. (1).

PANAMA: *Chiriquí*: Boquete, U.M.M.Z. (4).

#### *Hyla regilla curta*

MEXICO: *Baja California Sur*: Cabo San Lucas, M.C.Z. (1), U.S.N.M. (17); Cañon Cantiles, U.S.N.M. (1); Comondú, U.S.N.M. (2); Isla Coronado, M.C.Z. (1); La Paz (5); Miraflores, A.M.N.H. (16); Rancho de Parras, 19 kilometers south of Loreto, A.M.N.H. (2); San Ignacio, A.M.N.H. (1), M.C.Z. (1), U.M.M.Z. (28); Soria, U.S.N.M. (12); Todos Santos, K.U. (11).

#### *Hyla regilla hypochondriaca*

MEXICO: *Baja California Norte*: Cañon de las Palmas, Sierra de Juárez, U.S.N.M. (1); 4 kilometers north of Descausa, U.M.M.Z. (1), 77 kilometers southeast of Ensenada, L.B.S.C. (2); Isla Cedros, A.M.N.H. (2), U.S.N.M. (52); La Grulla, U.S.N.M. (1); Laguna Hanson, Sierra de Juárez, L.B.S.C. (1); Mattomi, F.M.N.H. (1); Playa Estero, 14.4 kilometers south of Ensenada, A.M.N.H. (8); Punta Clara, U.M.M.Z. (1); Rosario, U.M.M.Z. (2); San Quintín, U.S.N.M. (1); Sierra San Pedro Martir, U.S.N.M. (19); Texate, U.S.N.M. (15); Tijuana, A.M.N.H. (2).

#### *Hyla rivularis*

COSTA RICA: *Alajuela*: Chinchona, K.U. (18, 7 tadpoles), U.S.C. (7); between Chinchona and Salto El Angel, U.S.C. (4); Río Poasito, 1 kilometer north of Poasito, K.U. (21, 4 skeletons, 1 tadpoles); Salto El Angel, U.S.C. (2); 10 kilometers south of Varablanca, U.S.C. (2); 22.5 kilometers northwest of Varablanca, U.M.M.Z. (1 tadpoles); 1.6 kilometers south of Zapote, U.S.C. (10); 8 kilometers north of Zarcero, U.S.C. (3). *Cartago*: 1.6 kilometers northeast of Casa Mata, U.S.C. (1); 1 kilometer east of Pacayas, U.S.C. (1); Santa Cruz, U.S.C. (7); Volcán Turrialba, 1380 meters, U.M.M.Z. (14); Volcán Turrialba, 2175 meters, U.M.M.Z. (1). *Heredia*: El Gallito, Volcán Barba, A.N.S.P. (1), U.S.N.M. (3); Hacienda Cayuga, 1 kilometer north of Montaña Azul, K.U. (3, 1 tadpoles) 5 kilometers south of Los Cartagos, K.U. (3, 4 tadpoles); 3 kilometers north of Montaña Azul, K.U. (1 tadpole); Rama Sur of Río Las Vueltas, K.U. (11, 1 tadpoles), U.S.C. (19); San José de la Montaña, K.U. (1); 2.7 kilometers north of San José de la Montaña, K.U. (3 tadpoles), U.S.C. (1); 1.6 kilometers north-northeast of Uvita, U.S.C. (25); Volcán Barba, A.N.S.P. (4). *Puntarenas*: Monteverde, U.S.C. (26). *San José*: Cerro de la Muerte, M.C.Z. (2), U.S.C. (5); El Copey, A.N.S.P. (1); La Hondura, U.M.M.Z. (1); 2 kilometers north of Las Nubes, K.U. (3, 1 tadpoles); 18.7 kilometers north of San Isidro el General, U.M.M.Z. (15).

PANAMA: *Bocas del Toro*: north slope of Cerro Pando, 1920-2100 meters, K.U. (41). *Chiriquí*: Finca Bambito, 6 kilometers east-northeast of El Volcán, K.U. (3); Finca Ojo de Agua, southeast slope of Cerro La Pelota, K.U. (1); Quebrada Chevo, south slope of Cerro La Pelota, K.U. (9); south slope of Cerro Santa Catalina, 8 kilometers northwest of El Volcán, K.U. (9, 1 tadpole).

#### *Hyla robertmertensi*

MEXICO: *Chiapas*: Acacoyagua, U.S.N.M. (8); 2 kilometers west of Acacoyagua, U.M.M.Z. (203); 32 kilometers north of Arriaga, K.U. (6, 2 skeletons), 32 kilometers southeast of Arriaga, U.I.M.N.H. (2); Asunción, F.M.N.H. (5), U.I.M.N.H. (7), U.S.N.M. (1); 5 kilometers east of Huixtla, U.I.M.N.H. (15); La Esperanza, U.S.N.M. (16); 17 kilometers south of Las Cruces, K.U. (25, 1 eggs); 8.5 kilometers north

of Puerto Madero, U.M.M.Z. (2); 11.7 kilometers north of Puerto Madero, U.M.M.Z. (1); Tapachula, F.M.N.H. (1), U.I.M.N.H. (1); 11 kilometers south of Tapachula, K.U. (14, 1 skeleton); Tonalá, F.M.N.H. (7), U.I.M.N.H. (1); 16 kilometers southeast of Tonalá, U.I.M.N.H. (1). *Oaxaca*: Tapanatepec, U.M.M.Z. (2); 1.6 kilometers east of Tapanatepec, U.M.M.Z. (14); 4.3 kilometers east of Tapanatepec, U.I.M.N.H. (2); 7.5 kilometers west of Tapanatepec, U.M.M.Z. (39); 12.8 kilometers west of Tapanatepec, K.U. (8); 7.2 kilometers west-northwest of Zanatepec, U.M.M.Z. (77); 13.6 kilometers west-northwest of Zanatepec, T.N.H.C. (10); 22.7 kilometers west-northwest of Zanatepec, T.N.H.C. (7).

GUATEMALA: *Jutiapa*: Jutiapa, U.M.M.Z. (1); La Trinidad, U.M.M.Z. (23). *Retalhuecu*: Casa Blanca, U.M.M.Z. (1).

EL SALVADOR: *La Libertad*: 16 kilometers northwest of Santa Tecla, K.U. (1). *San Salvador*: 21.9 kilometers north of San Salvador, U.M.M.Z. (6).

#### *Hyla robertsoni*

MEXICO: *Hidalgo*: 16 kilometers west of Agua Buena, U.M.M.Z. (6); El Chico Parque Nacional, F.M.N.H. (2), K.U. (49, 5 skeletons), M.C.Z. (2), U.I.M.N.H. (45), U.M.M.Z. (6, 1 tadpoles), U.S.N.M. (25); 3.3 kilometers north of Zacualtipán, K.U. (1, 1 tadpoles); 8.5 kilometers southeast of Zacualtipán, K.U. (1 tadpoles). *Puebla*: Honey, U.M.M.Z. (1).

#### *Hyla rosenbergi*

COSTA RICA: *Puntarenas*: Cerro Puntado, 2 kilometers northeast of Jacó, U.S.C. (1); Dominical, U.U. (3); Colfito, K.U. (20, 2 skeletons), U.M.M.Z. (3), U.S.C. (6); 3 kilometers east of Colfito, K.U. (4), 11 kilometers east of Colfito, K.U. (2 skeletons), U.S.C. (1); Palmar Sur, K.U. (3); 2.5 kilometers southeast of Palmar Sur, K.U. (3); 4 kilometers southeast of Palmar Sur, K.U. (2); Rincón de Osa, U.M.M.Z. (4); U.S.C. (8), 4.5 kilometers west of Rincón de Osa, K.U. (4); Río Ferruviosa, 4.5 kilometers south of Rincón de Osa, U.M.M.Z. (2), U.S.C. (1). *Villa Neilly*, K.U. (1); 1 kilometer west-northwest of Villa Neilly, U.S.C. (1); 7 kilometers west-northwest of Villa Neilly, U.S.C. (2); 10.5 kilometers west-northwest of Villa Neilly, K.U. (2, 1 skeleton); 22 kilometers west-northwest of Villa Neilly, U.S.C. (5).

PANAMA: *Canal Zone*: Alhajuela, U.M.M.A. (1); Camp Chagres, K.U. (83; 5 kilometers northwest of Camboa, K.U. (1); Madden Dam, U.M.M.Z. (3); San Pablo, M.C.Z. (1); Summit Cardens, K.U. (1). *Chiriquí*: Puerto Armuelles, A.M.N.H. (2), A.N.S.P. (2). *Darién*: Camp Creek, below Yavisa, A.M.N.H. (25, 4 tadpoles); Cana, U.S.N.M. (1); Chalichimans Creek, Río Subcutí, A.M.N.H. (1); Río Esnape, M.C.Z. (1); Río Membrillo, mouth, A.M.N.H. (1); Río Chucunaque, 7 kilometers above Río Mortí, K.U. (3); Río Chucunaque, 10 kilometers below Río Subcutí, K.U. (3); Río Chucunaque at Río Ucurganí, U.S.N.M. (2); Río Sansón, A.M.N.H. (1); Río

Tuira at Río Mono, K.U. (25, 2 skeletons); Tacarcuna, K.U. (6); Three Falls Creek, below Yavisa, A.M.N.H. (2). *Los Santos*: Tonosí (3). *Panamá*: Bejuco, Río Bejuco, A.M.N.H. (1); 6 kilometers west-southwest of Chepo, K.U. (5); Río Bayano, F.M.N.H. (1), U.S.N.M. (1).

#### *Hyla rostrata*

PANAMA: *Canal Zone*: No specific locality, A.M.N.H. (3), T.N.H.C. (6); between Catuncillo and Cuayabalito, A.M.N.H. (1); 11 kilometers northwest of Miraflores Locks, T.N.H.C. (1); Road K2, T.N.H.C. (2). *Panamá*: 3 kilometers west-southwest of Chepo, K.U. (9, 2 tadpoles); 6 kilometers west-southwest of Chepo, K.U. (4), M.C.Z. (2); La Jolla, A.M.N.H. (1); 1.5 kilometers southwest of Naranjal, K.U. (1, 1 skeleton); 9 kilometers northeast of Pacora, K.U. (1); 2 kilometers north of Tocumen, K.U. (5, 1 skeleton); 8 kilometers northeast of Tocumen, K.U. (9). *San Blas*: Sasardí, K.U. (1).

#### *Hyla rubra*

PANAMA: *Canal Zone*: No specific locality, U.S.N.M. (1); Madden Dam, F.M.N.H. (1); San Pablo, M.C.Z. (2). *Colón*: Achioté, U.F. (13); Cerro Bruja, M.C.Z. (1). *Darién*: El Real, U.S.N.M. (2); Yavisa, M.V.Z. (8). *Panamá*: Juan Díaz, M.C.Z. (1); Las Sabanas, M.C.Z. (1); Río Trinidad, U.S.N.M. (1); 17 kilometers east of Tocumen, M.V.Z. (1).

#### *Hyla rufioculis*

COSTA RICA: *Alajuela*: Cinchona, K.U. (21), U.M.M.Z. (2); 5 kilometers south of Ciudad Quesada, U.S.C. (1). *Cartago*: Moravia de Turrialba, K.U. (107, 3 skeletons), M.C.Z. (3); Morehouse Finca, 7 kilometers south of Turrialba, F.M.N.H. (4), K.U. (17); Río Chitaría, 3 kilometers north-northeast of Pavones, U.S.C. (3); Turrialba, K.U. (13, 1 skeleton). *Guanacaste*: El Silencio, U.S.C. (4). *Heredia*: Isla Bonita, F.M.N.H. (6), K.U. (13), M.C.Z. (1). *Limón*: El Tigre, 12-20 kilometers southwest of Siquirres, U.S.C. (6); Río Lari at Río Dipnari, 21 kilometers southwest of Amubri, L.A.C.M. (1). *Puntarenas*: Finca Loma Linda, 2 kilometers southwest of Cañas Cordas, (1); 3.6 kilometers east of Monteverde, U.S.C. (1). *San José*: south slope of Cerro de la Muerte, 1540 meters, U.S.C. (3); Río Claro at Río La Hondura, U.S.C. (10); 13 kilometers north of San Isidro el General, K.U. (12), U.M.M.Z. (3), U.S.C. (1); 14 kilometers north of San Isidro el General, K.U. (13), U.M.M.Z. (13); 15 kilometers west-southwest of San Isidro el General, K.U. (45, 5 skeletons, 5 tadpoles), U.M.M.Z. (11), U.S.C. (58); 17.2 kilometers west-southwest of San Isidro el General, U.S.C. (2).

#### *Hyla rufitela*

NICARAGUA: No specific locality, U.S.N.M. (2). *Zelaya*: El Recreo, K.U. (1); Machuca, A.N.S.P. (2); Maselina Creek, A.M.N.H. (2).

COSTA RICA: *Heredia*: Puerto Viejo, U.C.R.

(2). *Limón*: La Castilla, A.N.S.P. (15); Río Tortuguero, 3 kilometers from mouth, A.M.N.H. (1). *Puntarenas*: Colfite, K.U. (2, 1 tadpoles); 4.5 kilometers west of Rincón de Osa, K.U. (1 tadpoles).

PANAMA: *Bocas del Toro*: Cayo de Agua, G.M.L. (1), K.U. (3); Isla Colón, K.U. (1); Península Valiente, Bluefields, K.U. (2); Río Cahuita, mouth, K.U. (8). *Canal Zone*: Barro Colorado Island, A.N.S.P. (7), F.M.N.H. (7), K.U. (11, 1 skeleton, 7 tadpoles, 1 eggs), T.N.H.C. (1), U.M.M.Z. (3). *Colón*: Achioté, K.U. (10). *Panama*: Río Puente, M.C.Z. (1). *Veraguas*: Río Concepción, mouth, K.U. (1).

#### *Hyla salvadorensis*

EL SALVADOR: *Santa Ana*: Hacienda Montecristo, Cerro Metapán, K.U. (1 tadpoles); Hacienda Los Planes, U.I.M.N.H. (1); Rancho San José, K.U. (3, 1 skeleton, 2 tadpoles).

HONDURAS: *Francisco-Morazán*: West slope of Cerro Uyuca, A.M.N.H. (14), K.U. (6, 1 skeleton), U.M.M.Z. (1).

#### *Hyla sartori*

MEXICO: *Guerrero*: 23.2 kilometers north of Acapulco, U.I.M.N.H. (4); 5 kilometers east of Acapulco, A.M.N.H. (2); Colonia Buenos Aires, 23 kilometers east of Tecpán de Galeana, U.M.M.Z. (7); El Limoncito, F.M.N.H. (16), U.M.M.Z. (1), U.S.N.M. (1); El Treinta, F.M.N.H. (1), U.I.M.N.H. (3); Laguna Coyuca, A.M.N.H. (1); La Venta, M.C.Z. (1); Marijonares, U.I.M.N.H. (11); 1.6 kilometers north of Organos, F.M.N.H. (2), U.I.M.N.H. (2); 19.2 kilometers south of Petaquillas, U.I.M.N.H. (1); 6.1 kilometers east of Tecpán de Galeana, T.N.H.C. (13); 11.2 kilometers west-northwest of Tierra Colorado, U.I.M.N.H. (1); 11.8 kilometers west-northwest of Tierra Colorada, U.M.M.Z. (51, 3 skeletons); Zacualpán, U.M.M.Z. (6). *Jalisco*: 6.4 kilometers northeast of La Resolana, K.U. (17); 24 kilometers northeast of La Resolana, K.U. (4). *Oaxaca*: 3 kilometers north of Poehutla, K.U. (1); 11.3 kilometers north of Poehutla, U.I.M.N.H. (4); 13.4 kilometers north of Poehutla, U.M.M.Z. (40).

#### *Hyla siopela*

MEXICO: *Veracruz*: west slope of Cofre de Perote, K.U. (36, 3 skeletons), U.I.M.N.H. (15).

#### *Hyla smaragdina*

MEXICO: *Colima*: Paso del Río, U.M.M.Z. (2). *Michoacán*: 6 kilometers east of Cojumatlán, F.M.N.H. (19), M.C.Z. (1), U.M.M.Z. (1); 1.6 kilometers north of Copuyo, T.C.W.C. (4); 8 kilometers north of Copuyo, T.C.W.C. (3); 17 kilometers east of Dos Aguas, U.M.M.Z. (22); Ostula, U.M.M.Z. (8); Pómaro, U.M.M.Z. (3); Salitre de Estopilas, U.M.M.Z. (7). *Morelos*: Tepoztlán, U.I.M.N.H. (1). *Nayarit*: Santa Barbara, L.A.C.M. (1 tadpoles). *Sinaloa*: Co-

pala, K.U. (7); Potrerillos, K.U. (2 tadpoles); Santa Lucía, K.U. (43, 3 skeletons), L.B.S.C. (31).

#### *Hyla smithii*

MEXICO: *Colima*: Armeria, U.M.M.Z. (1); 3 kilometers southwest of Colima, U.M.M.Z. (3); 5 kilometers south of Colima, K.U. (1); 72 kilometers southwest of Colima, M.V.Z. (2); Manzanillo, A.M.N.H. (1, 1 skeleton); 16 kilometers north of Manzanillo, C.A.S. (2); 5 kilometers east of Manzanillo, A.M.N.H. (2); 41.7 kilometers northwest of Manzanillo, M.V.Z. (1); Paso del Río, F.M.N.H. (1), U.I.M.N.H. (1), U.M.M.Z. (9); Periquillo, U.M.M.Z. (23); Queseria, F.M.N.H. (7), M.C.Z. (2), U.I.M.N.H. (7), U.M.M.Z. (17); Río Astillero, C.A.S. (1); 7 kilometers southwest of Tecolapa, U.M.M.Z. (3); 10 kilometers north of Trapichillos, U.M.M.Z. (1). *Guerrero*: Acahuiztota, T.C.W.C. (32); Acapulco, T.C.W.C. (2), U.M.M.Z. (1); 13 kilometers north of Acapulco, T.N.H.C. (2); 24 kilometers north of Acapulco, F.M.N.H. (39), U.I.M.N.H. (29); 26 kilometers north of Acapulco, T.N.H.C. (2); 27 kilometers northeast of Acapulco, U.I.M.N.H. (1); Agua del Obispo, F.M.N.H. (11), T.C.W.C. (5), U.I.M.N.H. (11), U.M.M.Z. (12), U.S.N.M. (16); 2 kilometers north of Agua del Obispo, T.C.W.C. (5); 4 kilometers south of Ahuolonga, T.C.W.C. (5); 5 kilometers west of Bajos de Ejido, U.M.M.Z. (1); Buena Vista, F.M.N.H. (1); 5 kilometers south of Buena Vista, A.M.N.H. (9); Chilpancingo, M.C.Z. (7); 19 kilometers south of Chilpancingo, F.M.N.H. (2); 1.6 kilometers southwest of Colotlipa, T.C.W.C. (2); 13.3 kilometers northwest of Coyuca, U.I.M.N.H. (7); El Limoncito, F.M.N.H. (3), U.I.M.N.H. (3); El Treinta, F.M.N.H. (21), U.I.M.N.H. (17); 22.4 kilometers south of Ixtapán de Sal (Mexico), K.U. (8); Laguna Coyuca, A.M.N.H. (2); 2.5 kilometers north of Mazatlán, U.I.M.N.H. (1), U.M.M.Z. (32); 14.4 kilometers south of Mazatlán, F.M.N.H. (8), U.I.M.N.H. (9); Monjonaros, U.I.M.N.H. (9); 4-6 kilometers north of Ocotito, K.U. (2), T.C.W.C. (10), U.M.M.Z. (5); Palo Blanco, F.M.N.H. (2), U.I.M.N.H. (2); 19 kilometers south of Petaquillas, U.I.M.N.H. (3); 10 kilometers west of Pie de la Guesta, U.M.M.Z. (1); 19 kilometers south of Puente de Ixtla (Morelos), F.M.N.H. (34), U.I.M.N.H. (22); Rincón, T.C.W.C. (3); 2 kilometers southeast of San Andrés de la Cruz, K.U. (2), U.M.M.Z. (1); San Vicente, K.U. (10); 17 kilometers south of Taxco, T.C.W.C. (2); 26 kilometers east of Tecpán de Galeana, T.N.H.C. (6); Tierra Colorada, T.C.W.C. (3), U.S.N.M. (7); 7 kilometers south of Tierra Colorada, U.M.M.Z. (2); 12 kilometers west-southwest of Tierra Colorada, U.M.M.Z. (10); 2 kilometers east of Tixtla, K.U. (2); Xaltiangui, F.M.N.H. (1); 5 kilometers east of Zacatula, U.M.M.Z. (1). *Jalisco*: Autlán road (kilometer 133), F.M.N.H. (4), U.I.M.N.H. (7); 5 kilometers east of Autlán, F.M.N.H. (1); south of Autlán, U.I.M.N.H. (6); Barro de Navidad, K.U. (14); 48 kilometers northeast of Barro de Navidad, M.V.Z. (8); 5 kilometers



- east of Barro de Navidad, U.M.M.Z. (1); 5 kilometers northwest of Barro de Navidad, K.U. (1); 6.4 kilometers northwest of Barro de Navidad, K.U. (4); 12.8 kilometers northeast of La Huerta, K.U. (5); 3 kilometers northeast of La Resolana, U.M.M.Z. (19); 6 kilometers northeast of La Resolana, K.U. (12); 3 kilometers southwest of La Resolana, K.U. (4); 8 kilometers east of Melaque, K.U. (10). *Michoacán*: Angililla, U.M.M.Z. (14); Apatzingán, F.M.N.H. (15), M.C.Z. (2), U.I.M.N.H. (46), U.M.M.Z. (9), U.S.N.M. (25); 1.6 kilometers east of Apatzingán, U.M.M.Z. (4); 8.6 kilometers east of Apatzingán, U.M.M.Z. (5); 24.5 kilometers east of Apatzingán, U.M.M.Z. (1) between Apatzingán and Uruapan, C.A.S. (19); 1.6 kilometers north of Arteaga, U.M.M.Z. (1); 13 kilometers south of Arteaga, U.M.M.Z. (1 tadpoles); 21 kilometers south of Arteaga, U.M.M.Z. (1 tadpoles); 2 kilometers south of Charapendo, U.M.M.Z. (5); 3 kilometers north-northeast of Coalcomán, U.M.M.Z. (5); El Sabino, F.M.N.H. (16), U.I.M.N.H. (13); La Playa de Jorullo, U.M.M.Z. (6); 11.2 kilometers south of Lombaria, U.M.M.Z. (1); Playa Azul, U.M.M.Z. (1); between Río Marquez and Cuatro Caminos, K.U. (9); Salitre de Estiopilas, U.M.M.Z. (1). *Morelos*: Alpuyecá, U.I.M.N.H. (4); Antiguo, F.M.N.H. (1); 3.5 kilometers west of Cuautlixco, K.U. (6); Cuernavaca, T.C.W.C. (8), U.I.M.N.H. (3), U.S.N.M. (1); 2.7 kilometers east of Cuernavaca, T.N.H.C. (9); 3 kilometers south, 8.8 kilometers east of Cuernavaca, T.C.W.C. (6); Huajintlán, F.M.N.H. (3), U.I.M.N.H. (2); 2 kilometers south of Jonacatepec, T.C.W.C. (21); Progreso, T.C.W.C. (13), U.I.M.N.H. (1); Puente de Ixtla, T.C.W.C. (1), U.I.M.N.H. (74), U.M.M.Z. (3), U.S.N.M. (25); 1 kilometer east of Puente de Ixtla, K.U. (6), T.C.W.C. (16); Temilpa, T.C.W.C. (26), Temoac, T.C.W.C. (4); 17 kilometers west of Yauatepec, T.C.W.C. (2); Zacatepec, T.C.W.C. (18); 3 kilometers west of Zacatepec, T.C.W.C. (18); U.I.M.N.H. (2). *Nayarit*: 21.6 kilometers south of Acaponeta, U.I.M.N.H. (20); 29.5 kilometers south of Acaponeta, U.I.M.N.H. (49); 47 kilometers south of Acaponeta, T.N.H.C. (2); Arroyo de Rifilón, 9 kilometers north of Compostela, C.A.S. (30); Cinco de Mayo, C.A.S. (4); 56 kilometers south of Escuinapa (Sinaloa), K.U. (3); 5 kilometers southeast of Huáicori, K.U. (1); 1.6 kilometers east of Ixtlán del Río, U.M.M.Z. (1); 4.3 kilometers east of Ixtlán del Río, C.A.S. (1); 6.4 kilometers east-southeast of Ixtlán del Río, K.U. (12); La Libertad, 16 kilometers northeast of San Blas, U.M.M.Z. (11); Navarrete, L.B.S.C. (6); 2 kilometers east of Navarrete, C.A.S. (2), T.N.H.C. (1); 3.5 kilometers southwest of Navarrete, C.A.S. (15), T.N.H.C. (15); Petaquilla, A.M.N.H. (1); Rancho Buenas Aires, 25 kilometers west of Tepic, A.M.N.H. (2); Río San Cayetano, 5 kilometers east of Tepic, A.M.N.H. (9); San Blas, C.A.S. (13), L.B.S.C. (1), M.V.Z. (1), U.I.M.N.H. (4); 1-8 kilometers northeast of San Blas, K.U. (7); 4 kilometers northeast of San Blas, L.B.S.C. (1); 5 kilometers northeast of San Blas, C.A.S. (3); 7-16 kilometers northeast of San Blas, C.A.S. (8); 1.6 kilometers southwest of San José del Conde, U.M.M.Z. (9); 2.4 kilometers east of Santa Cruz, C.A.S. (6); 14.5 kilometers east of Santa Cruz, C.A.S. (17); 4.5 kilometers west of Santa María del Oro, C.A.S. (9); Tepic, A.M.N.H. (2), C.A.S. (16), F.M.N.H. (17), U.I.M.N.H. (15), U.M.M.Z. (5); 29 kilometers north of Tepic, U.F. (1); 35 kilometers north of Tepic, C.A.S. (32), M.V.Z. (2); 9 kilometers east of Tepic, A.M.N.H. (2); 19 kilometers southeast of Tepic, K.U. (11); 37 kilometers southeast of Tepic, L.B.S.C. (32); 5.5 kilometers south of Tepic, A.M.N.H. (5); 8 kilometers east of Villa Hidalgo, C.A.S. (1); 2 kilometers west of Yago, C.A.S. (3). *Oaxaca*: Chacalapa, K.U. (2); La Candelaria, K.U. (57); 2.5 kilometers south of La Candelaria, K.U. (2); Mira León, U.I.M.N.H. (1); 3 kilometers north of Pochutla, K.U. (36, 5 skeletons); 11 kilometers north of Pochutla, A.M.N.H. (1); 13.4 kilometers north of Pochutla, U.M.M.Z. (1); 22.2 kilometers north of Pochutla, U.M.M.Z. (1); 28.2 kilometers north of Pochutla, U.M.M.Z. (10); 17 kilometers north of San Gabriel Mixtepec, K.U. (7); 5.7 kilometers south of San Gabriel Mixtepec, K.U. (1). *Puebla*: 10 kilometers southwest of Izúcar de Matamoros, K.U. (24). *Sinaloa*: 35 kilometers north of Acaponeta (Nayarit), U.I.M.N.H. (8); Chele, U.M.M.Z. (7); 4 kilometers northeast of Concordia, K.U. (1); 5 kilometers east of Concordia, C.A.S. (6), L.B.S.C. (1); 10 kilometers southwest of Concordia, K.U. (6); 18 kilometers northeast of Copala, U.I. (2); 3.2 kilometers southwest of Copala, K.U. (32); Culiacán, L.B.S.C. (3), U.F. (1); 12.1 kilometers north of Culiacán, U.M.M.Z. (1); 13.6 kilometers northwest of Culiacán, A.M.N.H. (1); Eldorado, U.I.M.N.H. (12); El Venadillo, U.M.M.Z. (3); 34 kilometers southeast of Escuinapas, K.U. (5); 7.3 kilometers southwest of Matatán, K.U. (3); Mazatlán, L.B.S.C. (1); 11.3 kilometers north of Mazatlán, L.B.S.C. (1); 32.3 kilometers north-northwest of Mazatlán, U.M.M.Z. (1); 14.7 kilometers south of Mazatlán, L.B.S.C. (1); U.I.M.N.H. (47); Plumosas, K.U. (3); Río Paxtala, L.B.S.C. (2); 5 kilometers southeast of Rosario, U.I.M.N.H. (1); 19 kilometers northeast of San Benito, K.U. (1); San Ignacio, K.U. (5); Teacapán, Isla Palmito del Verde, K.U. (1); 10 kilometers north-northwest of Teacapán, K.U. (1); Villa Unión, K.U. (7); 10 kilometers northeast of Villa Unión, K.U. (1); 41.6 kilometers northeast of Villa Unión, L.B.S.C. (8); 3.7 kilometers east of Villa Unión, K.U. (15, 1 eggs), L.B.S.C. (4).

#### *Hyla staufferi altae*

PANAMA: *Canal Zone*: 2.8 kilometers southwest of Fort Kobbe, K.U. (1); Road K2, T.N.H.C. (37); Summit, A.N.S.P. (4), F.M.N.H. (1), M.C.Z. (1), U.M.M.Z. (1). *Chiriquí*: 14.4 kilometers east of Concepción, A.M.N.H. (3); David, A.M.N.H. (1); 6 kilometers north of David, A.M.N.H. (1); 2.8 kilometers south of David, A.M.N.H. (1). *Coclé*: 1 kilometer northeast of El Caño, K.U. (3); El Valle, A.M.N.H. (21), A.N.S.P. (1), K.U. (15); 6 kilometers

ters south-southwest of Penonome, K.U. (13); 7 kilometers south-southwest of Penonome, K.U. (3). *Los Santos*: Tonosí, K.U. (5, 1 tadpoles). *Panamá*: 5 kilometers south of Bejuco, A.M.N.H. (2); 2 kilometers west-southwest of Chepo, K.U. (9), 6 kilometers west-southwest of Chepo, K.U. (4); Nueva Gorgona, A.M.N.H. (2); 1.6 kilometers west of Nueva Gorgona, A.M.N.H. (4); 9 kilometers northeast of Pacora, K.U. (4); 1.5 kilometers west of Pacora, K.U. (5); Panamá, K.U. (3); 2 kilometers north of Tocumen, K.U. (7); 8 kilometers northeast of Tocumen, K.U. (1).

*Hyla staufferi staufferi*

MEXICO: *Campeche*: Balchacaj, U.I.M.N.H. (5); Champotón, M.C.Z. (2), U.M.M.Z. (8); 5 kilometers south of Champotón, K.U. (2); Ciudad Carmen, U.I.M.N.H. (1); Encarnación, F.M.N.H. (11), U.I.M.N.H. (21); 6 kilometers west of Escárcega, K.U. (2); 7.5 kilometers west of Escárcega, K.U. (9); 13 kilometers west, 1 kilometer north of Escárcega, K.U. (6); Matamoros, F.M.N.H. (1); Pacaitun, Río Candelaria, F.M.N.H. (2); Tres Brazos, U.I.M.N.H. (3); Tuxpeña, U.M.M.Z. (1). *Chiapas*: No specific locality, U.M.M.Z. (1); Acacoyagua, U.S.N.M. (6); 2 kilometers west of Acacoyagua, U.M.M.Z. (5); 32 kilometers north of Arriaga, K.U. (4); 32 kilometers south of Arriaga, U.I.M.N.H. (2); Asunción, C.A.S. (1), U.I.M.N.H. (5); Berriozabal, U.M.M.Z. (1); Buena Vista, U.M.M.Z. (7); El Real, 34 kilometers northeast of Altamirano, T.C.W.C. (1); 6 kilometers northeast of Escuintla, U.M.M.Z. (1); 3 kilometers east of Finca Juárez, U.I.M.N.H. (22); 4 kilometers north of Ixtapa, K.U. (6); 3 kilometers southwest of Las Cruces, K.U. (1); 17 kilometers south of Las Cruces, K.U. (2); 24 kilometers south of Las Cruces, K.U. (1 tadpoles); 25 kilometers east, 5.6 kilometers north of Ocozacoautla, U.I.M.N.H. (4); west of Ocozacoautla, U.I.M.N.H. (14); Palenque, U.I.M.N.H. (4), U.S.N.M. (24); 1.6 kilometers south of Pichucualo, U.I.M.N.H. (1); Puerto Arista, U.I.M.N.H. (11); 8.5 kilometers north of Puerto Madero, K.U. (5); Rancho Monserrate, U.I.M.N.H. (3); Rancho San Bartolo, U.I.M.N.H. (13); Región Soconusco, U.I.M.N.H. (2); 2 kilometers south of Río de las Salmas, U.M.M.Z. (5); 11 kilometers south of Tapachula, K.U. (8); Tonalá, U.I.M.N.H. (7); 8 kilometers west of Tuxtla Gutierrez, U.M.M.Z. (3). *Guerrero*: Acapulco, U.M.M.Z. (2); 9 kilometers northwest of Acapulco, U.F. (1); 13 kilometers north of Acapulco, T.N.H.C. (2); 5 kilometers west of Bajos del Ejido, U.M.M.Z. (1); El Limoncita, F.M.N.H. (3), U.I.M.N.H. (10); Laguna Coyuca, A.M.N.H. (1); Mexcala, U.I.M.N.H. (1); 1.6 kilometers north of Organos, U.I.M.N.H. (1); Puerto Marques, A.M.N.H. (4); 5 kilometers east of Zacatula, U.M.M.Z. (1). *Morelos*: 3 kilometers south, 8.8 kilometers east of Cuernavaca, T.G.W.C. (1). *Oaxaca*: Chivela, A.M.N.H. (1); 11.8 kilometers south of Chivela, U.M.M.Z. (1); Huilotepec, A.M.N.H. (5); Juchitán, U.M.M.Z. (3); La Mata, U.I.M.N.H. (1); La Venta, U.I.M.N.H. (10); 78 kilometers north of

La Venta, T.N.H.C. (22); Loma Bonita, F.M.N.H. (1); Matías Romero, A.M.N.H. (3); 6.6 kilometers north of Matías Romero, U.I.M.N.H. (1); Nisa Pipi, 8 kilometers northwest of Tehuantepec, U.M.M.Z. (100); 3 kilometers north of Pochutla, K.U. (22, 4 skeletons); 13.4 kilometers north of Pochutla, U.M.M.Z. (1); 1.3 kilometers south of Pochutla, U.M.M.Z. (1); 2.5 kilometers south of Pochutla, K.U. (3); 5 kilometers south of Pochutla, K.U. (7); San Gerónimo, U.I.M.N.H. (1); 4.4 kilometers north of Sarabia, U.M.M.Z. (11); 6 kilometers south of Sarabia, U.M.M.Z. (2); Sierra Madre, north of Zanatepec, U.I.M.N.H. (2); 1.6 kilometers east of Tapanatepec, U.I.M.N.H. (40); 3 kilometers east of Tapanatepec, K.U. (26); 4.3 kilometers southwest of Tapanatepec, U.I.M.N.H. (1); 17.6 kilometers west-northwest of Tapanatepec, K.U. (2); Tehuantepec, A.M.N.H. (14), U.I.M.N.H. (26), U.M.M.Z. (36), U.S.N.M. (18); 3 kilometers east of Tehuantepec, U.M.M.Z. (9); 8 kilometers northeast of Tehuantepec, A.M.N.H. (1); 4 kilometers west of Tehuantepec, U.M.M.Z. (1); Temascal, U.S.C. (8); 3 kilometers south of Toluca, K.U. (2); Tuxtepec, K.U. (9, 1 tadpoles), U.I.M.N.H. (60); 3 kilometers south of Tuxtepec, U.I.M.N.H. (41); 13 kilometers south of Tuxtepec, U.I.M.N.H. (1); 17 kilometers south of Tuxtepec, K.U. (3); 21 kilometers south of Tuxtepec, U.I.M.N.H. (8); 27 kilometers south of Tuxtepec, U.I.M.N.H. (3); 3 kilometers south of Uvero, U.M.M.Z. (1); 1 kilometer north of Valle Nacional, U.I.M.N.H. (1); 1 kilometer west of Zanatepec, K.U. (1 tadpoles); 7 kilometers west-northwest of Zanatepec, U.M.M.Z. (6). *Puebla*: San Diego, A.M.N.H. (1); 30 kilometers northeast of Villa Juárez, T.N.H.C. (2). *Quintana Roo*: Coba, U.M.M.Z. (1); Isla Cozumel, 3.5 kilometers north of San Miguel, K.U. (3). *San Luis Potosí*: Ciudad Valles, A.M.N.H. (1), U.I.M.N.H. (1). *Tabasco*: Teapa, U.M.M.Z. (13); 10 kilometers north of Teapa, U.M.M.Z. (1); 24 kilometers north of Teapa, U.M.M.Z. (6); 27 kilometers north of Teapa, U.M.M.Z. (1); Tenosique, U.I.M.N.H. (1); 3.5 kilometers south of Villahermosa, U.M.M.Z. (2); 17 kilometers south of Villahermosa, U.M.M.Z. (8). *Tamaulipas*: 6 kilometers southeast of Altamira, U.I.M.N.H. (2); Antiguo Morelos, U.I.M.N.H. (1); 1.6 kilometers east of Ghamal, U.M.M.Z. (1); 19 kilometers south of Ciudad Mante, T.N.H.C. (3); 25 kilometers north of El Limón, U.I.M.N.H. (1); 36.2 kilometers north of El Limón, U.I.M.N.H. (4); between El Limón and Llera, U.M.M.Z. (2); Gómez Farías, U.M.M.Z. (3); 5 kilometers southeast of Gómez Farías, U.M.M.Z. (1); Pano Ayutle, 8 kilometers northeast of Gómez Farías, U.M.M.Z. (4); Río Frio, 8 kilometers west of San Gerardo, U.M.M.Z. (5); 5 kilometers west of San Gerardo, U.M.M.Z. (7); 4 kilometers southeast of Tres Marías, U.I.M.N.H. (12). *Veracruz*: 21 kilometers north of Acayucan, U.I.M.N.H. (1); 6 kilometers northwest of Acayucan, U.M.M.Z. (7); below Acultzingo, U.M.M.Z. (2); 1.6 kilometers east-southeast of Alvarado, U.M.M.Z. (2); 8.4 kilometers west of Alvarado, U.M.M.Z. (3); 24.5 kilometers northwest of Alvarado, U.I.M.N.H. (3); 2.5 kilometers south-



southwest of Amatitlán, U.M.M.Z. (3); 5 kilometers south of Aquilera, U.M.M.Z. (1); Arroyo de las Palmas, 10 kilometers north of Córdoba, U.M.M.Z. (1); Boca del Río, U.I.M.N.H. (21); 1.6 kilometers south of Boca del Río, U.M.M.Z. (2); 11 kilometers south of Boca del Río, U.M.M.Z. (7); 3 kilometers southwest of Boca del Río, K.U. (1); 5 kilometers southwest of Boca del Río, K.U. (1); 6 kilometers west of Boca del Río, U.I.M.N.H. (1); 8 kilometers east of Cerro Gordo, T.C.W.C. (7); Ciudad Alemán, U.M.M.Z. (2); 8 kilometers southwest of Coatzacoalcas, U.M.M.Z. (1); Córdoba, U.M.M.Z. (1); 5 kilometers east-southeast of Córdoba, A.M.N.H. (1), K.U. (1 tadpoles), T.N.H.C. (3), U.F. (1); 7 kilometers east-southeast of Córdoba, U.M.M.Z. (8); 3 kilometers west of Corral Nuevo, U.I.M.N.H. (1); 2.2 kilometers east of Cosalecaque, U.M.M.Z. (8); Cosamaloapan, U.M.M.Z. (4); west of Cotaxtla, U.I.M.N.H. (1); Cruz Blanca, U.I.M.N.H. (3); Cuatulan, K.U. (6), M.C.Z. (2), U.I.M.N.H. (16), U.S.N.M. (1); Cuatutlan, U.M.M.Z. (30); El Chico, 11 kilometers south-southeast of Jalapa, F.M.N.H. (2); 3 kilometers north of El Tropido, U.I.M.N.H. (6); 6 kilometers east of Encero, U.I.M.N.H. (23); 1.6 kilometers east-northeast of Encinal, U.M.M.Z. (3); Hacienda Tamiahua, Cabo Rojo, K.U. (1); Huatusco, U.I.M.N.H. (5); 10 kilometers southeast of Hueyapan, U.M.M.Z. (1); Jalapa, U.I. (1); 6 kilometers southeast of Jalapa, U.M.M.Z. (1); 1.6 kilometers north of La Laja, U.I.M.N.H. (1); 21.6 kilometers south of Las Choapas, T.C.W.C. (2); 5 kilometers northwest of Lerdo de Tejada, U.M.M.Z. (1); 17 kilometers east of Martínez de la Torre, U.I.M.N.H. (1); 6 kilometers west of Martínez de la Torre, U.I.M.N.H. (1); 2 kilometers east-northeast of Mata Oscura, K.U. (1); 3 kilometers northeast of Novillero, U.M.M.Z. (5); 5.4 kilometers northeast of Novillero, U.M.M.Z. (1); Orizaba, U.S.N.M. (1); Otatitlán, U.I.M.N.H. (5); Palma Sola, U.S.N.M. (1); Paso del Macho, U.I.M.N.H. (3), U.M.M.Z. (1); 5 kilometers southeast of Paso del Toro, K.U. (1); Potrero, M.C.Z. (3), U.I.M.N.H. (2), U.M.M.Z. (37), U.S.N.M. (3); Potrero Viejo, F.M.N.H. (4), K.U. (32); U.I.M.N.H. (16), U.M.M.Z. (69), U.S.N.M. (21); Presidio, U.S.N.M. (2); Puente Nacional, U.I.M.N.H. (2); Rodríguez Clara, U.I.M.N.H. (1); San Andrés Tuxtla, U.I.M.N.H. (1); 38 kilometers north of San Andrés Tuxtla, U.M.M.Z. (1); 10 kilometers east of San Juan de la Punta, M.C.Z. (1), U.I.M.N.H. (8), U.S.N.M. (15); Santiago Huatusco, U.M.M.Z. (2); Sauzla, U.M.M.Z. (4); 62 kilometers south of Tampico (Tamaulipas), U.I.M.N.H. (10); 19 kilometers north of Tempoal, U.I.M.N.H. (1); Tierra Colorada, U.I.M.N.H. (3); Tula, U.I.M.N.H. (3); 2.7 kilometers northwest of Tula, U.M.M.Z. (2); Veraacruz, A.M.N.H. (1); 5 kilometers south of Veracruz, U.M.M.Z. (3); 24 kilometers west of Veracruz, U.I.M.N.H. (17); Yanga, U.I.M.N.H. (2).

BRITISH HONDURAS: *Belize*: Belize, F.M.N.H. (1). *Cayo*: 6 kilometers south of Cayo, M.C.Z. (2); San Augustin, U.M.M.Z. (8). *Stann Creek*: 10 kilometers east of Stann Creek, U.M.M.Z. (1); between

Stann Creek and Roaring Creek, U.M.M.Z. (1); 5 kilometers south of Waha Loaf Creek, M.C.Z. (1).

GUATEMALA: *Alta Verapaz*: Chinajá, K.U. (1); Cubilquitz, U.M.M.Z. (8). *Baja Verapaz*: 1 kilometer south of San Geronimo, U.M.M.Z. (21). *Chiquimula*: 1.6 kilometers southeast of Chiquimula, U.M.M.Z. (2); Esquipulas, U.M.M.Z. (18). *El Petén*: Dolores, U.M.M.Z. (1); La Libertad, F.M.N.H. (2), K.U. (1), M.C.Z. (2), U.M.M.Z. (66), U.S.N.M. (2); Paso de Caballo, U.M.M.Z. (1); 1 kilometer south of Poptún, U.M.M.Z. (1); Sacluc, U.S.N.M. (1); Santa Teresa, U.M.M.Z. (4). *Eseuintla*: Cuyuta, 20 kilometers north of San José, A.M.N.H. (8). *Guatemala*: 16 kilometers northeast of Guatemala, K.U. (1). *Izabal*: Puerto Barrios, T.C.W.C. (14), U.M.M.Z. (10); 2.5 kilometers northeast of Rio Blanco, K.U. (2). *Jalapa*: Jalapa, U.M.M.Z. (44). *Jutiapa*: Finca La Trinidad, U.M.M.Z. (28); Jutiapa, U.M.M.Z. (2). *Zacapa*: 14 kilometers east-northeast of Mayuelas, K.U. (1); 7 kilometers east-northeast of Rio Hondo, K.U. (2, 1 tadpoles).

EL SALVADOR: *Cuscatlán*: 8 kilometers west-northwest of Cojutepeque, T.N.H.C. (3); 11.5 kilometers west-northwest of Cojutepeque, T.N.H.C. (4). *La Libertad*: Quetzaltepeque, C.A.S. (1); 16 kilometers northwest of Santa Tecla, K.U. (2). *La Unión*: 2.4 kilometers east of Santa Rosa, T.C.W.C. (2). *Morazán*: Divisadero, U.S.N.M. (5). *San Salvador*: San Salvador, F.M.N.H. (6), K.U. (17, 1 eggs), U.M.M.Z. (7); 1.6 kilometers northwest of San Salvador, K.U. (2); 21.9 kilometers north of San Salvador, U.M.M.Z. (1).

HONDURAS: *Atlántida*: Ceiba, U.S.N.M. (1); Tela, M.C.Z. (1). *Choluteca*: Choluteca, K.U. (6); 1.9 kilometers east of Choluteca, U.M.M.Z. (7); 3 kilometers east of Choluteca, K.U. (2); 6.2 kilometers east of Choluteca, K.U. (11); 10 kilometers east of Choluteca, K.U. (1); 5 kilometers south of Choluteca, Colón: Laguna Ebano, F.M.N.H. (1), M.C.Z. (1); Patuca, U.S.N.M. (1). *Comayagua*: 6.9 kilometers northwest of Siguatepeque, T.N.H.C. (1); 12 kilometers northwest of Siguatepeque, K.U. (1). *Cortes*: Lago de Yojoa, K.U. (7), M.C.Z. (1), T.C.W.C. (2). *El Paraíso*: Valle de Jamastran, A.M.N.H. (5). *Francisco Morazán*: 8.6 kilometers northwest of Comayagua, K.U. (1); El Zamorano, A.M.N.H. (10), K.U. (1), M.C.Z. (4); 29.3 kilometers north of Tegucigalpa, T.N.H.C. (2).

NICARAGUA: *Chinandega*: Finca San Isidro, 10 kilometers south of Chinandega, K.U. (23). *Managua*: 13 kilometers east of Managua, K.U. (1), U.M.M.Z. (8); 2 kilometers south of Tipitapa, K.U. (5). *Rivas*: Rivas, M.C.Z. (2); 9.5 kilometers southeast of Rivas, K.U. (1); 16 kilometers southeast of Rivas, M.C.Z. (12); 18 kilometers southeast of Rivas, K.U. (1); 7.7 kilometers northeast of San Juan del Sur, K.U. (8); 16.5 kilometers northeast of San Juan del Sur, K.U. (6); 5 kilometers southeast of San Pablo, K.U. (11). *Zelaya*: El Recreo, K.U. (19); Isla Grande del Maiz, K.U. (4); Wounta Haulover, A.N.S.P. (2).



COSTA RICA: *Alajuela*: Los Chiles, U.S.C. (3). *Guanacaste*: 4 kilometers west of Bagaces, U.S.C. (5); Finca Taboga, 20 kilometers southeast of Las Cañas, K.U. (2); 1.6 kilometers north of Cuayabo de Bagaces, U.S.C. (3); Cuardia, Río Tempisque, U.S.C. (1); 10 kilometers north of Cuardia, K.U. (2); 12 kilometers south of La Cruz, U.S.C. (1); Las Cañas, K.U. (1 skeleton); 27 kilometers north of Las Cañas, U.S.C. (5) Liberia, K.U. (13); 6 kilometers north of Liberia, U.S.C. (1); 8 kilometers north of Liberia, K.U. (1); 14.5 kilometers north of Liberia, U.S.C. (3); 14.5 kilometers south of Liberia, U.S.C. (5); 4 kilometers K.U. (1); 8.6 kilometers east-southeast of Playa del Coco, U.S.C. (14); 21 kilometers east-southeast of Playa del Coco, U.S.C. (2); Santa Cruz U.S.C. (2); Tenorio, K.U. (1); Tilarán, K.U. (1). *Puntarenas*: 6 kilometers east of Esparta, K.U. (1); 4 kilometers west-northwest of Esparta, K.U. (1); 10 kilometers west-northwest of Esparta, K.U. (8, 2 skeletons); 12 kilometers west-northwest of Esparta, K.U. (1); Hotel Maribella, K.U. (2); 10.8 kilometers north, 3 kilometers west of Puntarenas, T.C.W.C. (8).

#### *Hyla subocularis*

PANAMA: *Darién*: Laguna, K.U. (13); Río Chucunaque, A.M.N.H. (1); Río Chucunaque at first creek above Río Tuquesa, A.M.N.H. (1); Río Ucurgantí, 7 kilometers above mouth, K.U. (1, 1 tadpoles); Tacarcuna, K.U. (45, 3 skeletons), U.M.M.Z. (1).

#### *Hyla sumichrasti*

MEXICO: *Chiapas*: 10 kilometers northeast of Los Amates, U.I.M.N.H. (4); 19 kilometers north of Arriaga, U.M.M.Z. (3, 2 tadpoles); El Sumidero, U.I.M.N.H. (1); Finca San Bartolo, U.I.M.N.H. (8); Ocozacoatlán, U.I.M.N.H. (4); 4.5 kilometers northeast of Ocozacoatlán, U.I.M.N.H. (18); 26 kilometers east, 5.6 kilometers north of Ocozacoatlán, U.I.M.N.H. (3). Pitutal, south of Ocozacoatlán, U.I.M.N.H. (6), T.C.W.C. (1); 2 kilometers northwest of Pueblo Nuevo Solistahuacán, K.U. (42, 3 skeletons); Tonolá, U.I.M.N.H. (6). *Oaxaca*: Arroyo Palmar, U.I.M.N.H. (1); Cerro San Pedro del Istmo, U.I.M.N.H. (2); Cerro Santa Lucía, U.I.M.N.H. 11.8 kilometers south of Chivela, U.M.M.Z. (18, 1 skeleton); Llano Ocotál, C.A.S. (1), F.M.N.H. (12), U.I.M.N.H. (4); Portillo Nejapa, A.M.N.H. (2), K.U. (13, 1 tadpoles); Santa Efigenia, U.S.N.M. (5); 16 kilometers east of Tapanatepec, U.I.M.N.H. (1); Tres Cumbres, U.I.M.N.H. (1); between Zapotitlán and Huamelula, F.M.N.H. (3), U.I.M.N.H. (1).

#### *Hyla taeniopus*

MEXICO: *Hidalgo*: Tianguistengo, F.M.N.H. (4); 2.5 kilometers southwest of Tianguistengo, K.U. (3); 4 kilometers southwest of Tianguistengo, K.U. (1); 3 kilometers west of Xochicoatlán, K.U. (8, 2 skeletons). *Puebla*: 8.7 kilometers southwest of Huachinango, U.M.M.Z. (1); 11.7 kilometers southwest of Huachinango, U.M.M.Z. (1); Río Octapa, 3.7 kilometers north-northeast of Tezuitlán, K.U. (15, 4

skeletons, 1 tadpoles); 1.6 kilometers west of Teteles, T.N.H.C. (1); 8 kilometers northeast of Tezuitlán, K.U. (1); 1.5 kilometers southwest of Tlatlauquitepec, K.U. (1); 3 kilometers northwest of Zacapoaxtla, U.M.M.Z. (2). Veracruz: Barranca Texola, 16 kilometers southeast of Jalapa, U.I.M.N.H. (1); Huatusco, K.U. (1); 3 kilometers southwest of Huatusco, K.U. (3). U.M.M.Z. (3, 1 skeleton); 7.5 kilometers southwest of Huatusco, U.M.M.Z. (9, 1 skeleton); Jalapa, B.M.N.H. (1); 2 kilometers west of Jico, K.U. (5), U.M.M.Z. (2).

#### *Hyla thorectes*

MEXICO: *Oaxaca*: 30 kilometers north of San Gabriel Mixtepec, K.U. (1); 37 kilometers north of San Gabriel Mixtepec, K.U. (11, 2 skeletons, 3 tadpoles, 3 eggs), U.M.M.Z. 10.

#### *Hyla thysanota*

PANAMA: *Darién*: Cerro Mali, U.S.N.M. (1).

#### *Hyla tica*

COSTA RICA: *Alajuela*: Cinchona, K.U. (9), M.C.Z. (3); 5 kilometers south of Ciudad Quesada, U.S.C. (1); Río María-Aguilar, 3 kilometers west of Cariblanco, K.U. (1); 1.6 kilometers south of Zapote, U.S.C. (1); east slope of Volcán Poás, 21.3 kilometers north of Varablanca, U.M.M.A. (1). *Cartago*: Río Playas, U.S.C. (4); Tapantí, K.U. (21, 1 skeleton, 2 tadpoles), U.S.C. (9); Volcán Turrialba, 1385 meters, U.M.M.Z. (5). *Heredia*: 2 kilometers north of Cinco Esquinas, K.U. (1); San José de la Montaña, U.M.M.Z. (1); 5.6 kilometers south of Varablanca, T.N.H.C. (1). *Puntarenas*: 1 kilometer northeast of Monteverde, U.S.C. (5); 1 kilometer west of Monteverde, U.S.C. (1). *San José*: 2 kilometers north of Las Nubes, K.U. (1); Río Claro at Río La Honda, U.S.C. (10); Río Tarrazu, 1 kilometer south of San Cristóbal, U.S.C. (1); 15 kilometers north of San Isidro el General, K.U. (2).

PANAMA: *Chiriquí*: south slope of Cerro Santa Catalina, 8 kilometers northwest of El Volcán, K.U. (1, 1 skeleton); Finca Bambito, 6 kilometers east-northeast of El Volcán, K.U. (1); Finca Ojo de Agua, southeast slope of Cerro La Pelota, K.U. (2); Finca Palosanto, 7 kilometers north-northwest of El Volcán, K.U. (7); Quebrada Chevo, south slope of Cerro La Pelota, K.U. (17); Río Colorado, 17.5 kilometers northwest of El Volcán, K.U. (1); 14.5 kilometers north-northwest of El Volcán, K.U. (1); 16 kilometers north-northwest of El Volcán, K.U. (1).

#### *Hyla uranochroa*

COSTA RICA: *Alajuela*: Cinchona, K.U. (6, 2 skeletons, 8 tadpoles), U.S.C. (5); between Cinchona and Salto El Angel, U.S.C. (1); Ciudad Quesada, U.S.C. (1); San Carlos, U.S.N.M. (1); north slope of Volcán Poás, 22.5 kilometers north of Varablanca, U.M.M.Z. (1 tadpole); 1.6 kilometers south of Zapote, U.S.C. (2). *Cartago*: Moravia de Turrialba, K.U. (10,

1 skeleton); 1 kilometer east of Pacayas, U.S.C. (1); 3 kilometers south of Pavones, K.U. (18, 1 tadpoles); Río Chitaria, 3 kilometers north-northeast of Pavones, K.U. (1 tadpoles); Río Izaquito, near Pavones, U.S.C. (1); 4.3 kilometers northeast of Río Reventazón bridge, U.M.M.Z. (2 tadpoles); 3 kilometers north of Santa Rosa, K.U. (1 tadpoles); 1 kilometer north of Tapantí, U.S.C. (2); Turrialba, K.U. (1); Volcán Turrialba, U.M.M.Z. (1 tadpoles). *Heredia*: Cariblanco, K.U. (1); Hacienda Cayuga, 1 kilometer north of Montaña Azul, K.U. (1 tadpole), Isla Bonita, F.M.N.H. (1), K.U. (2, 1 tadpoles); Montaña Azul, K.U. (1 tadpoles); San José de la Montaña, K.U. (1); 2.7 kilometers north of San José de la Montaña, K.U. (2 tadpoles); 1.6 kilometers north-northeast of Uvita, U.S.C. (22). *Limón*: El Tigre, 12-20 kilometers southwest of Siquirres, U.S.C. (1); Pico Blanco, U.S.N.M. (1). *Puntarenas*: Esparta, M.C.Z. (1); Monteverde, U.S.C. (19). *San José*: south slope of Cerro de la Muerte, 1524 meters, U.S.C. (1); La Estrella, M.C.Z. (1); 1 kilometer west of La Honduras, U.S.C. (1); La Palma, A.N.S.P. (11), M.C.Z. (1), U.M.M.Z. (1), U.S.C. (4), U.S.N.M. (1); Río Tiriví, U.M.M.Z. (1); 14 kilometers north of San Isidro el General, U.M.M.Z. (1); 15 kilometers north of San Isidro el General, K.U. (3, 2 skeletons), U.M.M.Z. (2); 18.5 kilometers north of San Isidro el General, K.U. (5, 1 tadpoles), U.M.M.Z. (1).

PANAMA: *Boas del Toro*: north slope of Cerro Pando, 1450 meters, K.U. (26, 2 skeletons, 2 tadpoles); La Loma, M.C.Z. (6); Río Changena, 650 meters, K.U. (4); Río Changena, 830 meters, K.U. (4).

#### *Hyla valancifer*

MEXICO: *Veraeruz*: Volcán San Martín, K.U. (1); U.I.M.N.H. (1), U.M.M.Z. (2).

#### *Hyla walkeri*

MEXICO: *Chiapas*: 10 kilometers northwest of Comitán, K.U. (4); 14 kilometers northwest of Comitán, K.U. (3); 18 kilometers northwest of Comitán, K.U. (16, 2 skeletons, 1 tadpoles), M.C.Z. (2); El Suspiro, U.M.M.Z. (1); 2.5 kilometers south of Jitotól, K.U. (3, 1 tadpoles); 2 kilometers northwest of Pueblo Nuevo Solistahuacán, U.M.M.Z. (23); San Cristóbal de las Casas, U.I.M.N.H. (2); 8.8 kilometers southeast of San Cristóbal de las Casas, K.U. (1); 12.8 kilometers southeast of San Cristóbal de las Casas, K.U. (2); 6.4 kilometers northwest of San Cristóbal de las Casas, K.U. (1); 8.8 kilometers northwest of San Cristóbal de las Casas, U.M.M.Z. (11); 30 kilometers northwest of San Cristóbal de las Casas, U.M.M.Z. (20).

GUATEMALA: *El Quiché*: La Primavera, between Sacapulas and Santa Cruz Quiché, U.M.M.Z. (30); Ututlán, U.M.M.Z. (1). *Huehuetenango*: 3 kilometers north of San Juan Ixcay, U.M.M.Z. (32), 4 kilometers east of San Juan Ixcay, U.M.M.Z. (5); Soloma, U.M.M.Z. (28). *Jalapa*: Aserradero San Lorenzo, U.M.M.Z. (5).

#### *Hyla xanthosticta*

COSTA RICA: *Heredia*: south fork of Río Las Vueltas, south slope of Volcán Barba, K.U. (1).

#### *Hyla zeteki*

COSTA RICA: *Heredia*: Isla Bonita, K.U. (1); Varablanca, K.U. (1). *San José*: La Honduras, A.N.S.P. (5, 1 tadpoles); La Palma, K.U. (2), U.S.C. (2).

PANAMA: *Chiriquí*: Boquete, M.C.Z. (1), U.M.M.Z. (12, 1 skeleton), U.S.N.M. (1).

#### *Hyla* sp.

GUATEMALA: *Alta Verapaz*: Finca Los Alpes, K.U. (2 tadpoles), U.M.M.Z. (1 tadpoles).

#### *Pachymedusa dacnicolor*

MEXICO: *Colima*: No specific locality, F.M.N.H. (1), U.S.N.M. (1); Colima, A.M.N.H. (3), M.C.Z. (1), S.U. (1), U.I.M.N.H. (1), U.M.M.Z. (47); 3.7 kilometers north of Colima, A.M.N.H. (3, 1 skeleton); 1.6 kilometers southwest of Colima, A.I.M.N.H. (1); Hacienda Albarradita, U.M.M.Z. (4, 1 eggs); east of Lo de Villa, A.M.N.H. (1); Manzanilla, U.M.M.Z. (1); 33 kilometers southeast of Manzanillo, A.M.N.H. (2), K.U. (1), U.M.M.Z. (1); Paso del Río, U.I.M.N.H. (3); Periquillo, U.M.M.Z. (25); 1.6 kilometers south of Puebla Juárez, U.M.M.Z. (2); Querseria, U.M.M.Z. (2); Río Armería, U.M.M.Z. (1); Santiago, U.M.M.Z. (5); 8 kilometers southwest of Tecolapa, U.M.M.Z. (5, 1 eggs); 4 kilometers northwest of Tecmán, U.M.M.Z. (1); 5-8 kilometers northwest of Villa Alvarez, U.M.M.Z. (1). *Guerrero*: No specific locality, U.M.M.Z. (2); Acahuitzotla, K.U. (1), T.C.W.C. (1); U.M.M.Z. (1); Acapulco, A.M.N.H. (3), M.C.Z. (3), U.F. (1), U.M.M.Z. (1); 6.4 kilometers north of Acapulco, U.I.M.N.H. (1); 7.8 kilometers north of Acapulco, U.F. (1); 27 kilometers northeast of Acapulco, U.I. (3); 5 kilometers south of Buena Vista, A.M.N.H. (3); between Chilapa and Tixtla, K.U. (1); Chilpancingo, F.M.N.H. (1), M.C.Z. (25), U.M.M.Z. (7); Cocula, A.M.N.H. (2); 13.3 kilometers northwest of Coyuca, U.I.M.N.H. (1); Colonia Buenas Aires, 27 kilometers east of Tecpan, K.U. (1 skeleton), U.M.M.Z. (1); 1.6 kilometers southwest of Colotlipa, T.C.W.C. (6); 12 kilometers north of El Naranjo, U.M.M.Z. (1); 3 kilometers south of Garrapata, U.I.M.N.H. (1); Iguala, T.C.W.C. (4); 9 kilometers south of Mazatlán, U.I.M.N.H. (1); 8 kilometers north of Mexcala, U.I.M.N.H. (1); 1.6 kilometers southeast of Mochitlán, T.C.W.C. (2); Mojonares, U.I.M.N.H. (8); Ocotito, T.C.W.C. (4), U.I.M.N.H. (1); 5.4 kilometers north of Ocotito, U.M.M.Z. (3); Ometepe, U.S.N.M. (1); 1.6 kilometers north of Organos, U.I.M.N.H. (2); Palo Blanco, U.I.M.N.H. (3); 9.6 kilometers west of Pie de la Cuesta, U.M.M.Z. (3); Puerto Marquez, A.M.N.H. (2); Rincón, T.C.W.C. (1); Río Aguacatillo, 30 kilometers north of Acapulco, T.C.W.C. (1); 1.7 kilome-

ters south of San Andreas de la Cruz, K.U. (1); 17 kilometers south of Taxco, T.C.W.C. (3); 21 kilometers south of Taxco, T.C.W.C. (4); 32 kilometers east-southeast of Tecpan, U.I.M.N.H. (1); Tierra Colorada, U.S.N.M. (1); 10 kilometers north of Tierra Colorada, U.F. (1); 1.6 kilometers southwest of Tierra Colorada, T.C.W.C. (1); 8 kilometers southwest of Tierra Colorada, T.C.W.C. (7); 2 kilometers east of Tixtla, K.U. (7), T.N.H.C. (1); 5 kilometers east of Tixtla, U.F. (3). *Jalisco*: 5 kilometers northeast of Autlán, U.I.M.N.H. (2); 15 kilometers northwest of Cihuatlán, K.U. (1); 3 kilometers north of La Resolana, U.M.M.Z. (2), 6.6 kilometers northeast of La Resolana, K.U. (2); 32 kilometers southwest of La Resolana, K.U. (1); 16 kilometers southeast of Las Anonas, T.C.W.C. (5); 8 kilometers east of Melaque, K.U. (6); 3 kilometers west of Tamazula, A.M.N.H. (2). *Michoacán*: Aquililla, U.M.M.Z. (13); Apatzingán, F.M.N.H. (1), U.M.M.Z. (2); 1.6 kilometers east of Apatzingán, U.M.M.Z. (3); 10.4 kilometers east of Apatzingán, U.M.M.Z. (1); 14.4 kilometers east of Apatzingán, U.M.M.Z. (1); 23 kilometers south of Apatzingán, K.U. (1); 2 kilometers south of Charapendo, U.M.M.Z. (1); Coalhuayana, U.M.M.A. (3); Coalcomán, K.U. (5, 1 skeleton), U.M.M.Z. (55); El Sabino, U.I.M.N.H. (1); Huetano road, U.I.M.N.H. (2); La Placita, U.M.M.Z. (1); 32 kilometers east of Nueva Italia, U.M.M.Z. (2); between Río Marquez and Cuatro Caminos, K.U. (2); Salitre de Estopilas, U.M.M.Z. (2). *Morelos*: Alpuyeca, T.C.W.C. (1); 4 kilometers south of Alpuyeca, T.C.W.C. (6); 12 kilometers northwest of Axochiapan, T.C.W.C. (1); 3.5 kilometers west of Cuautlixco, K.U. (10, 4 skeletons); 5 kilometers northwest of Cuantlixco, U.M.M.Z. (2); 14 kilometers south of Cuernavaca, U.M.M.Z. (1); El Rodeo, T.C.W.C. (15); 2 kilometers south of Jonacatepec, T.C.W.C. (7); Puente de Ixtla, U.I.M.N.H. (1); 1 kilometer northeast of Puente de Ixtla, K.U. (3); T.C.W.C. (21); 19 kilometers south of Puente de Ixtla, U.I.M.N.H. (2); Temilpa, T.C.W.C. (4); 1.6 kilometers south of Temixco, U.M.M.Z. (2); Tequesquitengo, A.M.N.H. (1); Zaca-tepec, T.C.W.C. (12); 3 kilometers west of Zaca-tepec, T.C.W.C. (10). *Nayarit*: Aaponeta, A.M.N.H. (2), U.S.N.M. (2), T.C.W.C. (1); 30-50 kilometers south of Aaponeta, A.M.N.H. (2); 6.4 kilometers north of Compostela, A.M.N.H. (7); 6 kilometers south of Ixtlán del Río, U.M.M.Z. (1); Jesús María, A.M.N.H. (1); 8.6 kilometers northeast of Navarrete, U.F. (1); 10 kilometers south-southwest of Navarrete, M.V.Z. (1); Peñitas, A.M.N.H. (4); Rosamorada, A.M.N.H. (4); San Blas, A.M.N.H. (8), K.U. (4), U.I.M.N.H. (4), U.M.M.Z. (1); 2 kilometers north of San Blas, S.U. (2); 23 kilometers east of San Blas, U.I.M.N.H. (5); 8.6 kilometers south-southeast of San Blas, U.M.M.Z. (4); 1.6 kilometers southwest of San José del Conde, U.M.M.Z. (1); San Juan Peyotán, L.A.C.M. (1 tadpoles); 5 kilometers north of Santa Isabela, U.M.M.Z. (1); Santiago Esequintla, A.M.N.H. (2); Tepic, U.I.M.N.H. (2), U.M.M.Z. (6); 3 kilometers south of Tepic, A.M.N.H. (10); 5.5 kilometers south of Tepic, A.M.N.H. (1); 37 kilometers northwest

of Tepic, T.C.W.C. (1); 4 kilometers east of Tuxpan, K.U. (2); 11 kilometers southeast of Tuxpan, U.I.M.N.H. (2). *Oaxaca*: Chaealapa, K.U. (1); 4.2 kilometers north of Chaealapa, U.F. (2); Escurano, U.I. (1); La Candelaria, K.U. (4, 1 eggs); Mirador, A.M.N.H. (1); Pochutla, U.I.M.N.H. (8); 3 kilometers north of Pochutla, K.U. (1); 32.9 kilometers north of Pochutla, U.M.M.Z. (21), 41.4 kilometers north of Poehutla, U.M.M.Z. (1); 2.0 kilometers south of Pochutla, K.U. (3); U.M.M.Z. (10), 5 kilometers south of Poehutla, K.U. (4); Tehuantepec, U.S.N.M. (1). *Sinaloa*: 8 kilometers north of Carrizalejo, K.U. (15); Chele, U.M.M.Z. (1); Coneepeión, K.U. (1); Concordia, A.M.N.H. (1); 5 kilometers southwest of Concordia, K.U. (5), 3.2 kilometers southwest of Copala, K.U. (1); Costa Rica, 25 kilometers south of Culiacán, U.I.M.N.H. (2); Culiacán, U.M.M.Z. (1); 3 kilometers north of Culiacán, A.M.N.H. (1); 12 kilometers north of Culiacán, K.U. (1), U.M.M.Z. (1); 21 kilometers south of Culiacán, M.V.Z. (2); Eldorado, A.M.N.H. (2); 1.6 kilometers northeast of El Fuerte, F.M.N.H. (22); 13 kilometers northeast of El Fuerte, F.M.N.H. (1); Elota, K.U. (1); Escuinapa, A.M.N.H. (3); 22 kilometers southeast of Escuinapa, T.C.W.C. (1); 25 kilometers southeast of Escuinapa, U.M.M.Z. (5); El Venadillo, U.M.M.Z. (1); Guanacaste, 1.6 kilometers southwest of Palmer, M.V.Z. (1); Isla Palmito del Verde, middle, K.U. (1); 5 kilometers northeast of Las Trancas, K.U. (4); 5 kilometers north of Los Moehis, K.U. (1); 21 kilometers north-northeast of Los Mochis, U.I.M.N.H. (3); 7.3 kilometers southwest of Matatán, K.U. (9); Mazatlán, A.M.N.H. (1), U.I.M.N.H. (10), U.S.N.M. (1); 3-40 kilometers north-northwest Mazatlán, A.M.N.H. (3), A.N.S.P. (2), M.C.Z. (12), M.V.Z. (11), U.M.M.Z. (6); 3 kilometers east of Mazatlán, T.C.W.C. (1); 1 kilometer southeast of Mazatlán, M.C.Z. (1); 4 kilometers southeast of Navolato, K.U. (1); Presidio, S.U. (1), U.S.N.M. (1); Rosario, U.I.M.N.H. (10), U.S.N.M. (1); 13 kilometers west-northwest of Rosario, U.M.M.Z. (2); San Franciscoquito, A.M.N.H. (1); 5 kilometers southwest of San Ignacio, K.U. (4, 3 tadpoles); Teacapán, K.U. (1); Villa Unión, K.U. (37, 1 tadpoles), S.U. (6), U.M.M.Z. (1); 9.1 kilometers northeast of Villa Unión, K.U. (4); 3.7 kilometers east of Villa Unión, K.U. (1). *Sonora*: Alamos, A.M.N.H. (5), K.U. (2); Guiracoba, A.M.N.H. (5), M.V.Z. (11); 2.5 kilometers north of Navajoa, U.M.M.Z. (1); 5 kilometers northwest of Navajoa, U.M.M.Z. (1); Presa Obregon, K.U. (1); Río Alamos, 14.4 kilometers southeast of Alamos, K.U. (15).

#### *Phrynosoma venulosa*

MEXICO: *Campeche*: Beeán, M.C.Z. (1), U.M.M.Z. (1); Champotón, U.M.M.Z. (4); 5 kilometers south of Champotón, K.U. (5); 2.5 kilometers west of Escárcega, K.U. (1); 7.5 kilometers west of Escárcega, K.U. (2), U.M.M.Z. (1); 12 kilometers west of Escárcega, K.U. (1); 13 kilometers west, 1 kilometer north of Escárcega, K.U. (3); Laguna Silvitue, K.U. (1); Pacatún, Río Candelaria, F.M.N.H. (2); Ruinas Edzna, K.U. (1); Tres Brazos,



- F.M.N.H. (1), U.I.M.N.H. (1). *Chiapas*: Acacoyagua, U.S.N.M. (1); Colonia Soconusco, U.S.N.M. (2); Cruz de Piedra, U.S.N.M. (10), Escuintla, U.M.M.Z. (10); La Esperanza, U.M.M.Z. (2), U.S.N.M. (3); 8 kilometers north of Puerto Madero, U.M.M.Z. (1); 18 kilometers south of Teapa (Tabasco), U.I.M.N.H. (1). *Colima*: 1.6 kilometers north of Colima, U.M.M.Z. (1); 11-32 kilometers northwest of Manzanillo, M.V.Z. (1); Paso del Río, U.M.M.Z. (1); Río Astillero, C.A.S. (1). *Guerro*: La Venta, F.M.N.H. (3); Puerto Marquez, A.M.N.H. (2). *Michoacán*: Barranca de Bejuco, U.M.M.Z. (1). *Nayarit*: 74 kilometers south of Esquinapa (Sinaloa), K.U. (2); east of San Blas, U.I.M.N.H. (1); 8 kilometers east of San Blas, U.I.M.N.H. (1); 23 kilometers east of San Blas, K.U. (1); 29 kilometers north-northwest of Tepic, U.F. (2); 34 kilometers north-northwest of Tepic, K.U. (1 tadpoles), L.B.S.C. (16, 1 skeleton). *Oaxaca*: Matías Romero, A.M.N.H. (4); 45 kilometers north of Matías Romero, U.I.M.N.H. (1); Tapanatepec, M.C.Z. (3); Temascal, U.S.C. (1); Tuxtepec, U.S.N.M. (1); between Zanatepec and Tapanatepec, U.I.M.N.H. (1). *Quintana Roo*: 4 kilometers north-northeast of Felipe Carrillo Puerto, K.U. (1); 8 kilometers west of Puerto Juárez, K.U. (1); 13 kilometers west of Puerto Juárez, K.U. (1). *San Luis Potosí*: 1 kilometer east of El Naranjo, U.M.M.Z. (2); Pujal, L.S.U. (1); Río Coy near Pujal, U.S.N.M. (1); Tamazunchale, U.M.M.Z. (1); 4 kilometers north of Tamazunchale, U.M.M.Z. (1); 29 kilometers east of Tamuín, U.F. (1); 16 kilometers south of Valles, A.M.N.H. (1); 16 kilometers northwest of Xilitla, A.M.N.H. (1). *Sinaloa*: Presidio, B.M.N.H. (2). *Tabasco*: Cárdenas, U.M.M.Z. (1); 60 kilometers west of Cárdenas, K.U. (3); 4 kilometers northeast of Comalcalco, A.M.N.H. (3); Frontera, B.M.N.H. (2); 24 kilometers east of Frontera, M.C.Z. (1); 2.3 kilometers northeast of Huimanguillo, U.M.M.Z. (1); 5 kilometers north of Teapa, U.M.M.Z. (2); 13 kilometers north of Teapa, U.M.M.Z. (1); 21 kilometers north of Teapa, U.M.M.Z. (4); 25 kilometers north of Teapa, U.M.M.Z. (1); 29 kilometers north of Teapa, U.M.M.Z. (3); Tenosique, U.S.N.M. (1); 10 kilometers north, 24 kilometers west of Villahermosa, K.U. (2); 3.5 kilometers south of Villahermosa, U.M.M.A. (3). *Tamaulipas*: 6 kilometers north of El Mante, U.M.M.Z. (1); Río Sabinas, 5 kilometers northeast of Gómez Farías, U.M.M.Z. (1); Tampico, B.M.N.H. (5). *Veracruz*: 29 kilometers southeast of Alvarado, U.M.M.Z. (14); 38.4 kilometers southeast of Alvarado, U.M.M.Z. (1); 2.5 kilometers south-southwest of Amatitlán, U.M.M.Z. (12); Barranca Metlac, K.U. (1 skeleton); 5 kilometers southwest of Boca del Río, K.U. (6), U.I.M.N.H. (5); 6.6 kilometers southwest of Boca del Río, K.U. (5); 7 kilometers north-northwest of Cerro Cordo, K.U. (1); Chacaltanguis, U.M.M.Z. (1); Ciénega de Macuile, U.M.M.Z. (13); Ciudad Alemán, U.M.M.Z. (6); Córdoba, U.S.N.M. (2); 10 kilometers north of Córdoba, U.M.M.Z. (1); 17 kilometers east-southeast of Córdoba, T.N.H.C. (1); 21 kilometers north of Corral Nuevo, U.I.M.N.H. (12); Cosamaloapan, U.M.M.Z. (1); Cuatutlapan, U.M.M.Z. (2); Cuautlapan, F.M.N.H. (2), K.U. (48), U.M.M.Z. (50); 11 kilometers east of Ebano (San Luis Potosí), T.N.H.C. (2); El Potrero, M.C.Z. (2); Encinal, K.U. (1 tadpoles); 5.5 kilometers east-northeast of Encinal, U.M.M.Z. (1); Huatusco, U.I.M.N.H. (2); Jalapa, B.M.N.H. (1); 19 kilometers east of Jalapa, U.I.M.N.H. (3); 20 kilometers east-northeast of Jesús Carranza, K.U. (2); 20 kilometers south of Jesús Carranza, K.U. (4); 10 kilometers north of José Cardel, M.V.Z. (4); La Laja, U.I.M.N.H. (22); 2 kilometers northwest of Lerdo de Tejada, U.M.M.Z. (2); 16 kilometers west-northwest of Los Conejos, K.U. (3); 6 kilometers west of Martínez de la Torre, U.I.M.N.H. (1); Minatitlán, A.M.N.H. (1); 5 kilometers west-southwest of Minatitlán, U.M.M.Z. (1); Misantla, B.M.N.H. (5); 1.6 kilometers northeast of Novillero, U.M.M.Z. (1); 5 kilometers northeast of Novillero, U.M.M.Z. (1); Ozuluama, K.U. (1); Panuco, M.C.Z. (1), U.M.M.Z. (6); 5.5 kilometers northeast of Panuco, T.N.H.C. (1); Paraje Nuevo, U.M.M.Z. (16); Paso del Macho, U.I.M.N.H. (4), U.M.M.Z. (4); Peñuela, A.M.N.H. (1); Potrero Viejo, F.M.N.H. (1), K.U. (10), U.I.M.N.H. (2), U.M.M.Z. (23); Rodríguez Clara, F.M.N.H. (1); Salinas, T.C.W.C. (1); 20 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (1); 48 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (1); San Isidro, K.U. (1); 3 kilometers west of San Marcos, K.U. (3); Sausal, U.M.M.Z. (9); Tecolutla, U.I.M.N.H. (13); 5 kilometers south of Tehuatlán, K.U. (2); Tierra Colorada, F.M.N.H. (1), U.I.M.N.H. (1), Toxtlacuaya, F.M.N.H. (2); Tuxpam, A.M.N.H. (2), K.U. (1); Veracruz, A.M.N.H. (1), I.P.N. (1), U.F. (10), U.M.M.Z. (3); 6 kilometers west-southwest of Zacualpilla, K.U. (1). *Yucatán*: Chichén Itzá, F.M.N.H. (6), U.M.M.Z. (2).
- BRITISH HONDURAS: *Orange Walk*: 3 kilometers south of Corozal, M.C.Z. (1).
- GUATEMALA: *El Petén*: La Libertad, F.M.N.H. (2), M.C.Z. (1), U.M.M.Z. (30), U.S.N.M. (2). *Escuintla*: Cuyuta, A.M.N.H. (72). *Retalhuleu*: Caballo Blanco, F.M.N.H. (1); Casa Blanca, U.M.M.Z. (1). *Suchitepequez*: Mazatenango, C.A.S. (6). *Zacapa*: 23 kilometers west of Zacapa, T.C.W.C. (20).
- HONDURAS: *Comayagua*: La Misión, A.M.N.H. (1), M.C.Z. (1); 8 kilometers above La Misión, M.C.Z. (1). *Cortés*: Agua Azul, A.M.N.H. (2); 7 kilometers southwest of La Lima, K.U. (1); 1.6 kilometers west of La Lima, T.C.W.C. (5). *El Paraiso*: Valle de Jamastran, A.M.N.H. (1).
- NICARAGUA: No specific locality, U.S.N.M. (2). *Chinandega*: Finca San Isidro, 10 kilometers south of Chinandega, K.U. (4). *Managua*: 8 kilometers northwest of Managua, K.U. (2). *Matagalpa*: Hacienda La Cumplida, K.U. (1). *Zelaya*: Wounta Haulover, A.N.S.P. (1).
- COSTA RICA: *Alajuela*: Los Chiles, U.S.C. (4). *Guanacaste*: Bebedero, B.M.N.H. (1); Finca Tabogo, 20 kilometers southeast of Las Cañas, K.U. (1); Hacienda La Mojica, 3 kilometers south, 18 kilometers west of Las Cañas, T.C.W.C. (8); Las Huecas,

U.M.M.Z. (1); 17 kilometers north of Liberia, U.S.C. (1); 20 kilometers north of Liberia, U.S.C. (5); 33 kilometers north of Liberia, U.S.C. (1); Río Tenorio, 5 kilometers south, 16 kilometers west of Las Cañas, T.C.W.C. (1). *Puntarenas*: 4 kilometers west-northwest of Esparta, K.U. (26, 5 skeletons); Palmar Norte, K.U. (8, 1 skeleton); Palmar Sur, K.U. (3); Parrita, U.S.C. (1).

PANAMA: *Canal Zone*: No specific locality, M.C.Z. (1). Ancon, A.N.S.P. (1); La Pita, M.C.Z. (1); Madden Dam, S.U. (1); Madden Forest, K.U. (2). *Chiriquí*: Suma, Río San Pablo, A.M.N.H. (1). *Coclé*: Aguadulee, K.U. (1); Santa Clara, F.M.N.H. (1). *Colón*: Ciricito, C.A.S. (1). *Darién*: El Real, K.U. (2); Río Canelon at Río Chueunaque, U.M.M.Z. (12); Río Ucurgantí, 7 kilometers above mouth, K.U. (1). *Panamá*: 5 kilometers south of Bejuco, A.M.N.H. (2); 10 kilometers west-southwest of Chepo, K.U. (16); Nueva Gorgona, A.M.N.H. (3, 1 tadpoles), K.U. (1 tadpoles); Punta Paitilla, M.C.Z. (1); Tapia, A.M.N.H. (1).

#### Phyllomedusa lemur

COSTA RICA: *Alajuela*: Cinchona, K.U. (8, 1 tadpoles); 5 kilometers south of Ciudad Quesada, U.S.C. (1). *Cartago*: La Suiza, U.S.C. (1); Moravia, K.U. (22, 2 skeletons); Tapantí, K.U. (53, 4 skeletons), U.S.C. (1); 10 kilometers north of Río Reventazón bridge, U.S.C. (1). *Heredia*: Cariblanco, M.C.Z. (1); Isla Bonita, F.M.N.H. (1). *Limón*: El Tigre, 12-20 kilometers southwest of Siquirres, K.U. (1 tadpoles), U.S.C. (3, 1 tadpoles); junction of Río Lari and Río Dipari, 21 kilometers south of Amubre, U.S.C. (1). *Puntarenas*: 3.6 kilometers east of Monteverde, U.M.M.Z. (1), U.S.C. (1). *San José*: La Palma, A.N.S.P. (2), K.U. (22), M.C.Z. (2), U.M.M.Z. (5), U.S.C. (4), U.S.N.M. (1); Río Claro at Río Honduras, U.S.C. (1).

PANAMA: *Bocas del Toro*: Río Changena, 650 meters, B.Y.U. (2), K.U. (5); Río Changena, 830 meters, K.U. (1); Río Claro near junction with Río Changena, 910 meters, K.U. (7). *Coclé*: El Valle, A.N.S.P. (1). *Darién*: Cerro Malí, U.S.N.M. (1). *Panamá*: Cerro La Campana, K.U. (3).

#### Phyllomedusa venusta

PANAMA: *Darién*: Río Tuira at Río Mono, K.U. (4, 1 skeleton).

#### Plectrohyla avia

MEXICO: *Chiapas*: El Chiequite, Volcán Tacaná, U.I.M.N.H. (1); Región de Soconusco, K.U. (1 skeleton), U.I.M.N.H. (1); Volcán Tacaná, 8 kilometers north of Unión Juárez, K.U. (2).

GUATEMALA: *Quetzaltenango*: Granja Lorena, U.M.M.Z. (1).

#### Plectrohyla glandulosa

GUATEMALA: No specific locality, B.M.N.H. (2). *Huehuetenango*: Laguna de Vejcha, 5.5 kilome-

ters south of San Mateo Ixtatán, K.U. (1, 1 tadpoles); 3 kilometers south of Paquix, U.M.M.Z. (7); 8 kilometers south of Paquix, K.U. (111, 9 skeletons, 3 tadpoles); M.C.Z. (3); 1.5 kilometers east of San Mateo Ixtatán, K.U. (1 tadpoles); Todos Santos, U.M.M.Z. (2); 2.5 kilometers north of Toquiá, K.U. (2). *Jalapa*: 8 kilometers east of Mataquescuintla, La Soledad Grande, F.M.N.H. (11). *Quetzaltenango*: 37 kilometers southeast of Malacatancito, K.U. (1 tadpoles); 6 kilometers north of San Carlos Sija, K.U. (7). *San Marcos*: 1 kilometer east of Ixchiguan, U.M.M.Z. (1 tadpoles); 5 kilometers west of Ixchiguan, U.M.M.Z. (1 tadpoles); 2 kilometers northwest of Ixchiguan, M.C.Z. (1), U.M.M.Z. (6); Volcán Tajumulco, F.M.N.H. (1). *Sololá*: Los Encuentros, U.M.M.Z. (13). *Totonicapán*: Desconsuelo, U.M.M.Z. (1); María Tucum, U.M.M.Z. (1, 2 tadpoles), K.U. (1 tadpoles); 13.4 kilometers north of San Carlos Sija, K.U. (2).

EL SALVADOR: *Chalatenango*: Los Esemiles, M.V.Z. (1).

#### Plectrohyla guatemalensis

MEXICO: *Chiapas*: Chicomuselo, U.M.M.Z. (2); El Chiequite, Volcán, Tacaná, U.I.M.N.H. (1); Letrero, U.M.M.Z. (1); 3.6 kilometers south of Rayón Mesdalapa, K.U. (1 tadpoles); 5.6 kilometers south of Rayón Mescalapa, K.U. (1, 2 tadpoles); 6.2 kilometers south of Rayón Mescalapa, K.U. (7, 1 skeleton, 2 tadpoles); Región de Soconusco, U.I.M.N.H. (1); Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, K.U. (1); 18 kilometers north of Pueblo Nuevo Solistahuacán, K.U. (8), U.M.M.Z. (4); San Cristóbal de las Casas, A.M.N.H. (1), U.I.M.N.H. (1); 10 kilometers southeast of San Cristóbal de las Casas, M.V.Z. (4); 4 kilometers west of San Cristóbal de las Casas, U.M.M.Z. (2); Volcán Tacaná, 8 kilometers north of Unión Juárez, K.U. (2, 1 tadpoles).

GUATEMALA: *Alta Verapaz*: Finca Chichén, U.M.M.Z. (1 tadpoles); Finca Los Alpes, K.U. (11, 2 skeletons). *Baja Verapaz*: Cubulco, B.Y.U. (1). *Chimaltenango*: Teepán, A.M.N.H. (1 tadpoles). *El Quiché*: Nebaj, U.M.M.Z. (1 tadpoles). *Guatemala*: 11 kilometers east of San José Pinula, U.M.M.Z. (2 tadpoles). *Huehuetenango*: San Juan Ixcay, K.U. (1); 3 kilometers east of San Juan Ixcay, U.M.M.Z. (1). *Jalapa*: Aserradero San Lorenzo, U.M.M.Z. (3); 8 kilometers east of Mataquescuintla, La Soledad Grande, F.M.N.H. (1). *Quetzaltenango*: Granja Lorena, K.U. (1, 1 skeleton), U.M.M.Z. (1, 2 tadpoles); 10.5 kilometers west-southwest of San Martín Sacatepequez, K.U. (1). *San Marcos*: Río Achute below Tacaná, U.M.M.Z. (1 tadpoles); Tacaná, U.M.M.Z. (1); Tejutla, U.M.M.Z. (1). *Sololá*: Panajachél, M.C.Z. (1); 2 kilometers northwest of Panajachél, K.U. (1), U.M.M.Z. (2, 1 tadpoles); 1.6 kilometers southeast of Sololá, K.U. (1). *Totonicapán*: Momostenango, U.M.M.Z. (2); Totonicapán, U.S.N.M. (1 tadpoles).

HONDURAS: *Yoro*: Portillo Grande, F.M.N.H. (4).

EL SALVADOR: *Santa Ana*: Cerro Metapan, K.U. (1); Cerro Trifinio, K.U. (1); Hacienda Los Planes, K.U. (1); Hacienda Montecristo, K.U. (7); Miramundo, F.M.N.H. (3).

#### *Plectrohyla hartwegi*

MEXICO: *Chiapas*: Barrejonel, U.M.M.Z. (1); Parajé El Triunfo, K.U. (1). *Oaxaca*: Cerro Azul, U.I.M.N.H. (1).

#### *Plectrohyla ixil*

MEXICO: *Chiapas*: 3.6 kilometers south of Rayón Mescalapa, K.U. (1 tadpoles); 5.6 kilometers south of Rayón Mescalapa, K.U. (8, 1 skeleton); 6.2 kilometers south of Rayón Mescalapa, K.U. (28, 3 skeletons, 1 tadpoles), M.C.Z. (2); 4 kilometers northwest of Pueblo Nuevo Solistahuacán, U.M.M.Z. (2); 15 kilometers north of Pueblo Nuevo Solistahuacán, U.M.M.Z. (13); 18 kilometers north of Pueblo Nuevo Solistahuacán, K.U. (22), U.M.M.Z. (10); 28 kilometers north of Pueblo Nuevo Solistahuacán, U.M.M.Z. (1).

GUATEMALA: *El Quiché*: Finca San Francisco, U.M.M.Z. (5, 1 tadpoles); Finca Tesoro, U.M.M.Z. (1 tadpoles).

#### *Plectrohyla lacertosa*

MEXICO: *Chiapas*: Región de Soconusco, U.I.M.N.H. (1).

#### *Plectrohyla matudai*

MEXICO: *Chiapas*: Cerro Ovando, M.C.Z. (1), U.I.M.N.H. (1, 1 tadpoles), U.M.M.Z. (9, 1 skeleton, 3 tadpoles), U.S.N.M. (28); Cerro Tres Picos, U.I.M.N.H. (1); El Chiciquite, U.I.M.N.H. (2); El Fenix, U.M.M.Z. (3); El Rastrojo, U.I.M.N.H. (1); Monte Cristo, U.M.M.Z. (1); Región de Soconusco, C.A.S. (1), M.C.Z. (1); U.I.M.N.H. (9); Rodilla, 16 kilometers south of Ciltepec, U.M.M.Z. (3); Unión Juárez, U.I.M.N.H. (3). *Oaxaca*: Cerro Baul, U.I.M.N.H. (2); Río Ostuta, A.M.N.H. (4), K.U. (1); Sierra Madre above Zanatepec, U.I.M.N.H. (8); 19 kilometers north-northeast of Zanatepec, L.S.U. (1).

GUATEMALA: *Chimaltenango*: Acatenango, U.S.N.M. (12); Finca Recreo, U.M.M.Z. (1 tadpoles). *Guatemala*: 11 kilometers east of San José Pinula, K.U. (2 tadpoles). *Huehuetenango*: Finca Injerta, U.M.M.Z. (1). *San Marcos*: El Porvenir, F.M.N.H. (12); Finca La Paz, K.U. (3, 1 skeleton, 2 tadpoles), U.M.M.Z. (6, 2 tadpoles); Volcán Tajumulco, F.M.N.H. (2 tadpoles). *Suchitepequez*: Finca El Naranjo, west slope Volcán Santa Clara, U.I.M.N.H. (10).

#### *Plectrohyla pyenoehila*

MEXICO: *Chiapas*: 5 kilometers north-northwest of San Cristóbal de las Casas, T.C.W.C. (1). *Vera Cruz*: Coyame, A.M.N.H. (1) [probably erroneous locality].

#### *Plectrohyla queechi*

GUATEMALA: *Alta Verapaz*: Finca Chichén, U.M.M.Z. (2, 1 tadpoles); Finca Los Alpes, K.U. (9, 1 skeleton, 3 tadpoles), U.M.M.Z. (4, 1 tadpoles). *El Quiché*, Finca San Francisco, U.M.M.Z. (1 tadpoles).

#### *Plectrohyla sagorum*

MEXICO: *Chiapas*: Cerro Ovando, M.C.Z. (1), U.I.M.N.H. (2), U.M.M.Z. (16, 1 skeleton, 2 tadpoles), U.S.N.M. (18); Cerro Paschtal, U.M.M.Z. (1); Chicomuselo, U.M.M.Z. (10); El Chiciquite, U.I.M.N.H. (3); Monte Cristo, U.M.M.Z. (1); Parajé El Triunfo, K.U. (1); Región de Soconusco, U.I.M.N.H. (5); Volcán Tacaná, 8 kilometers north of Unión Juárez, K.U. (13).

GUATEMALA: *Quetzaltenango*: Granja Lorena, K.U. (3, 1 tadpoles), U.M.M.Z. (6, 2 tadpoles); 10.4 kilometers west-southwest of San Martín Sacatepequez, K.U. (2 tadpoles). *San Marcos*: Volcán Tajumulco, F.M.N.H. (5).

EL SALVADOR: *Chalatenango*: Los Esemiles, M.V.Z. (1).

#### *Pseudacris elarkii*

MEXICO: *Tamaulipas*: 8 kilometers west of Matamoros, S.U. (2).

#### *Pternohyla dentata*

MEXICO: *Aguascalientes*: 15 kilometers east of Aguascalientes, K.U. (4, 4 skeletons), U.I.M.N.H. (137); 20.6 kilometers east of Aguascalientes, K.U. (1); 26.2 kilometers east of Aguascalientes, U.I.M.N.H. (1). *Jalisco*: 13 kilometers northeast of Lagos de Moreno, U.I.M.N.H. (1).

#### *Pternohyla fodiens*

MEXICO: *Colima*: between Buena Vista and Salvador, U.M.M.Z. (1); Colima, M.C.Z. (2); Quiseria, U.M.M.Z. (1). *Jalisco*: 3-6 kilometers south of Acatlán, U.M.M.Z. (2); 8 kilometers west-southwest of Acatlán, K.U. (1); 26.4 kilometers northeast of Ameca U.I.M.N.H. (3); 3 kilometers northeast of Autlán, U.I.M.N.H. (4); 4 kilometers west of Ayoel Chica, U.I.M.N.H. (1); 51 kilometers northwest of Ayutla, K.U. (1); Chapala, A.M.N.H. (10, 1 skeleton); 1.6 kilometers north of Chapala, A.M.N.H. (1); 11.5 kilometers north of Chapala, U.I.M.N.H. (5); 16 kilometers north of Chapala, A.M.N.H. (1); 5 kilometers northwest of Degollado, K.U. (4); 16 kilometers northwest of Degollado, K.U. (2); Guadalajara, K.U. (1); 16 kilometers east of Guadalajara, U.I.M.N.H. (9); 28 kilometers south of Guadalajara,



U.I.M.N.H. (12); 21 kilometers south, 24 kilometers west of Guadalajara, K.U. (1); 29 kilometers north-west of Guadalajara, U.I.M.N.H. (2); 1.6 kilometers west of Ixtlahuacán, A.M.N.H. (1); 8 kilometers west of Ixtlahuacán, A.M.N.H. (1); Jamay, A.M.N.H. (69); Magdalena, A.M.N.H. (1), U.I.M.N.H. (11); 3 kilometers east-northeast of Magdalena, K.U. (1); 18 kilometers north of Santa Cruz, K.U. (7); 8 kilometers south of Santa Cruz, T.C.W.C. (20); 14 kilometers northeast of Tepatitlán, U.I.M.N.H. (22); 6 kilometers southwest of Tepatitlán, U.I.M.N.H. (3); 16 kilometers northwest of Tequila, T.C.W.C. (2); 19 kilometers northeast of Unión Tula, K.U. (1); 8 kilometers southwest of Unión Tula, K.U. (17, 1 skeleton). *Michoacán*: between Río Marquez and Cuatro Caminos, K.U. (2). *Nayarit*: Acaponeta, U.S.N.M. (1); 29-50 kilometers south of Acaponeta, A.M.N.H. (10); Ahuacatlán, T.C.W.C. (2); 56 kilometers south of Esquinapa (Sinaloa), K.U. (3); Ixtlán del Río, U.M.M.Z. (1); 1.6 kilometers east of Ixtlán del Río, K.U. (1); 5 kilometers southeast of Mirador, K.U. (1); Peñitas, A.M.N.H. (4); Río Acaponeta, 4 kilometers south-southwest of Acaponeta, A.M.N.H. (1); Río San Cayateno, 5.6 kilometers southeast of Tepic, A.M.N.H. (5); 3 kilometers southwest of Rosamorada, K.U. (3); Tepic, U.I.M.N.H. (2); 37 kilometers east of Tepic, M.V.Z. (1); 8.6 kilometers south-southeast of Tepic, U.M.M.Z. (9); 3 kilometers south of Tepic, S.U. (1); 34 kilometers north-northwest of Tepic, K.U. (1 tadpoles); 11 kilometers southeast of Tuxpan, U.I.M.N.H. (27). *Sinaloa*: Concordia, T.C.W.C. (1); 4 kilometers northeast of Concordia, K.U. (1); Costa Rica, 25 kilometers south of Culiacán, U.I.M.N.H. (7); Eldorado, A.M.N.H. (1); 1.6 kilometers northeast of El Fuerte, U.I.M.N.H. (4); 34 kilometers southeast of Esquinapas, K.U. (7); 21 kilometers northeast of Los Moehis, U.I.M.N.H. (5); Matatán, K.U. (4), 7.3 kilometers southwest of Matatán, K.U. (2); Mazatlán, M.C.Z. (6, 1 skeleton), U.I.M.N.H. (6); 1.6 kilometers north of Mazatlán, K.U. (2 tadpoles); 5.6 kilometers north of Mazatlán, U.M.M.Z. (28); 6-12 kilometers north of Mazatlán, U.M.M.Z. (1); 14.4 kilometers north of Mazatlán, U.I.M.N.H. (1); 31.4 kilometers north of Mazatlán, U.M.M.Z. (1); Rosario, K.U. (1), U.I.M.N.H. (4), U.S.N.M. (1); 5 kilometers southwest of San Ignacio, K.U. (1); 1.6 east-northeast of San Lorenzo, K.U. (2); Villa Unión, K.U. (14); 1 kilometer north of Villa Unión, K.U. (6 skeletons); 10 kilometers northeast of Villa Unión, K.U. (1); 3.7 kilometers east of Villa Unión, K.U. (6). *Sonora*: 5 kilometers north-northwest of Alamos, K.U. (1); 13 kilometers north-northwest of Alamos, U.I.M.N.H. (1); 13 kilometers north of Ciudad Obregon, K.U. (2); El Bamuri, S.U. (4); 13 kilometers north of El Oasis, U.M. (4); 45 kilometers east of Hermosillo, A.M.N.H. (2); 18.4 kilometers south of Hermosillo A.M. (2); 25 kilometers west of La Playa, S.U. (3); Magdalena, U.F. (2); 21 kilometers south of Masiaea, T.C.W.C. (5); 64 kilometers south of Navajoa, K.U. (1); 5 kilometers northwest of Navajoa, U.M.M.Z. (7); 8 kilometers north of Noria, S.U. (1), U.M.M.Z. (41); Trieheras, A.M.N.H. (5).

#### *Ptychohyla euthysanota euthysanota*

MEXICO: *Chiapas*: Cascarada, 30 kilometers west of Ciltapeec, U.M.M.Z. (2); Cerro Ovando, U.M.M.Z. (2); Chicomuselo, U.M.M.Z. (2); Finca Juárez, 28 kilometers north of Esequintla, U.S.N.M. (4); Las Nubes, Cerro Ovando, U.S.N.M. (9); Salto de Agua, U.S.N.M. (13). *Oaxaca*: Cerro Peeho Blanco, U.I.M.N.H. (1); between La Cloria and Cerro Azul, U.I.M.N.H. (2); Río Grande, A.M.N.H. (2); Santo Tomás Teepan, U.I.M.N.H. (1); Sierra Madre above Zanatepec, U.I.M.N.H. (3).

CUATEMALA: *San Marcos*: Finca La Paz, 2 kilometers west of La Reforma, K.U. (14, 1 skeleton, 3 tadpoles), M.C.Z. (1), U.M.M.Z. (1, 7 tadpoles); Finca Pirineos, Río Samalá, F.M.N.H. (1). *Santa Rosa*: Finca La Gloria, U.M.M.Z. (2 tadpoles). *Solola*: Finca Santo Tomás, U.M.M.Z. (1 tadpoles); Olas de Moeá, near Moeá, F.M.N.H. (1).

EL SALVADOR: *Chalatenango*: Los Esemiles, U.S.N.M. (1). *Santa Ana*: Miramundo, F.M.N.H. (1).

#### *Ptychohyla euthysanota macrotympanum*

MEXICO: *Chiapas*: 6 kilometers northeast of Chiapa de Corzo, T.C.W.C. (1); 16 kilometers east of Chiapa de Corzo, T.C.W.C. (1); 16 kilometers east of Chiapa de Corzo, A.M.N.H. (1); Linda Vista, 2 kilometers northwest of Pueblo Nuevo Solistahuacán, K.U. (2, 1 skeleton); Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, K.U. (2, 4 tadpoles); 18 kilometers northwest of Pueblo Nuevo Solistahuacán, K.U. (1); San Fernando, M.Z.T.G. (2); Tonina (ruins), K.U. (1).

CUATEMALA: *Huehuetenango*: Finca La Democracia, U.M.M.Z. (1, 2 tadpoles); Jacaltenango, U.M.M.Z. (3, 1 tadpoles); 2 kilometers west of San Pedro Neeta, U.M.M.Z. (1 tadpoles).

#### *Ptychohyla ignicolor*

MEXICO: *Oaxaca*: Campamento Vista Hermosa, K.U. (4, 1 tadpoles), U.M.M.Z. (1); 4.2 kilometers south of Campamento Vista Hermosa, K.U. (34, 1 skeleton, 2 tadpoles, 1 eggs), M.C.Z. (4), U.I.M.N.H. (2); 6 kilometers south of Campamento Vista Hermosa, K.U. (8, 1 skeleton), U.M.M.Z. (3); 8 kilometers south of Campamento Vista Hermosa, U.M.M.Z. (7).

#### *Ptychohyla leonhardschultzei*

MEXICO: *Guerrero*: Agua del Obispo, F.M.N.H. (4), M.C.Z. (1), U.I.M.N.H. (2), U.S.N.M. (1); Malinaltepec, Z.M.B. (2); 1.6 kilometers southeast of San Andreas de la Cruz, U.M.M.Z. (3). *Oaxaca*: Campamento Vista Hermosa, K.U. (8, 3 tadpoles), U.M.M.Z. (1); 2.5 kilometers north of La Soledad, K.U. (1); 30 kilometers north of San Gabriel Mixtepec, K.U. (22); 33 kilometers north of San Gabriel Mixtepec, K.U. (20), 37 kilometers north of San Gabriel Mixtepec, K.U. (7), M.C.Z. (5); San Lucas Camotlán, U.I.M.N.H. (1), U.S.N.M. (2); 10.4 kilo-

meters south of Valle Nacional, U.M.M.Z. (1 tadpoles); 22.7 kilometers south of Valle Nacional, U.M.M.Z. (5); 32.6 kilometers south of Valle Nacional, U.M.M.Z. (1); 5 kilometers south of Yetla, K.U. (1 tadpoles); 7.5 kilometers south of Yetla, K.U. (9, 2 skeletons, 4 tadpoles), U.M.M.Z. (2, 1 tadpoles); 9 kilometers south of Yetla, K.U. (1 tadpoles).

*Plectrohyla schmidtorum chamulae*

MEXICO: *Chiapas*: 32 kilometers north of Jitotol, U.I.M.N.H. (1); 15 kilometers north of Pueblo Nuevo Solistahuacán, U.M.M.Z. (4); 16.4 kilometers north of Pueblo Nuevo Solistahuacán, U.M.M.Z. (10); 18 kilometers north of Pueblo Nuevo Solistahuacán, K.U. (6), U.M.M.Z. (18); 18.6 kilometers north of Pueblo Nuevo Solistahuacán, K.U. (5), U.M.M.Z. (4); 5.6 kilometers south of Rayón Mescalapa, K.U. (1, 1 tadpoles); 6.2 kilometers south of Rayón Mescalapa, K.U. (17, 1 skeleton, 1 tadpoles), M.C.Z. (7); 5.6 kilometers south of Solusuchiapa, T.C.W.C. (1).

*Plectrohyla schmidtorum schmidtorum*

MEXICO: *Chiapas*: Finca Irlandia, U.M.M.Z. (2); Finca San Jerónimo, U.I.M.N.H. (2). *Oaxaca*: Sierra Madre above Zanatepec, U.I.M.N.H. (4).

GUATEMALA: *San Marcos*: El Porvenir, F.M.N.H. (3), U.M.M.Z. (1); Finca La Paz, 2 kilometers west of La Reforma, K.U. (29, 2 skeletons, 3 tadpoles), M.C.Z. (2), U.M.M.Z. (4 tadpoles).

*Plectrohyla spinipollex*

GUATEMALA: *Alta Verapaz*: Finca Chichén, U.M.M.Z. (1 tadpoles); Finca Los Alpes, K.U. (30, 3 skeletons, 2 tadpoles), M.C.Z. (2), U.M.M.Z. (4, 1 tadpoles); La Primavera, U.M.M.Z. (1 tadpoles); Panzamalá, U.M.M.Z. (1 tadpoles). *Baja Verapaz*: 32 kilometers north of Morazán, K.U. (1 tadpoles); Santa Elena, U.M.M.Z. (3). *Huehuetenango*: 1 kilometer east of Barillas, U.M.M.Z. (2 tadpoles). *Progreso*: Finca Bucaral, U.M.M.Z. (3, 1 skeleton, 1 tadpoles).

HONDURAS: *Atlántida*: mountains behind Ceiba, M.C.Z. (1). *Francisco Morazán*: Cerro Uyuca, A.M.N.H. (3), K.U. (1), U.M.M.Z. (2). *Yoro*: Portillo Grande, M.C.Z. (1).

NICARAGUA: *Matagalpa*: Finca Tepeyac, 10 kilometers north, 9 kilometers east of Matagalpa, K.U. (3 tadpoles); 2.5 kilometers east of Matagalpa, U.M.M.Z. (1); Santa María de Ostuma, K.U. (1).

*Smilisca baudinii*

MEXICO: No specific locality, M.N.H.N. (1). *Campeche*: Balchacaj, F.M.N.H. (4), U.I.M.N.H. (15); Champotón, U.M.M.Z. (4); 16 kilometers east of Champotón, U.M.M.Z. (1); 5 kilometers south of Champotón, K.U. (7); 10 kilometers south of Champotón, K.U. (4, 2 tadpoles); 24 kilometers south of Champotón, U.M.M.Z. (2); Chuina, K.U. (3); Ciudad del Carmen, U.I.M.N.H. (6); Dzibalchén, K.U. (19);

Encarnación, F.M.N.H. (14), U.I.M.N.H. (16); 1 kilometer west of Escárcega, K.U. (6); 7 kilometers west of Escárcega, K.U. (22); 14 kilometers west of Escárcega, K.U. (2); 3 kilometers north of Hopelchén, K.U. (3); Matamoros, F.M.N.H. (1); Pital, U.I.M.N.H. (1); 1 kilometer southwest of Puerto Real, Isla del Carmen, K.U. (20); Ruinas Edzna, K.U. (1); San José Carpizo, U.M.M.Z. (1); Tres Brazos, F.M.N.H. (1), U.I.M.N.H. (3); Tuxpeña Camp, U.M.M.Z. (1). *Chiapas*: Acacoyagua, U.S.N.M. (7); 5 kilometers east of Arroyo Minas, U.I.M.N.H. (5); Berriozabal, U.M.M.Z. (7); Chiapa de Corzo, U.M.M.Z. (2); Cintalapa, U.I.M.N.H. (1); Colonia Soconusco, U.S.N.M. (5); 5 kilometers west of Colonia Soconusco, U.M.M.Z. (7); Comitán, K.U. (1); El Suspiro, U.M.M.Z. (11); Escuintla, U.M.M.Z. (10); 6 kilometers northeast of Escuintla, U.M.M.Z. (26); 3 kilometers east of Finca Juárez, U.I.M.N.H. (1); Finca Prussia, U.M.M.Z. (1); Honduras, U.M.M.Z. (4); La Grada, U.M.M.Z. (1); 21 kilometers south of La Trinitaria, U.I.M.N.H. (2); 14.4 kilometers southwest of Las Cruces, K.U. (6), Palenque, U.I.M.N.H. (1), U.S.N.M. (12); 2 kilometers northwest of Pueblo Nuevo Solistahuacán, K.U. (3), U.M.M.Z. (9); 1.3 kilometers north of Puerto Madero, K.U. (4); 4 kilometers north of Puerto Madero, K.U. (2); 8 kilometers north of Puerto Madero, U.M.M.Z. (2); 12 kilometers north of Puerto Madero, K.U. (1); 17.6 kilometers north of Puerto Madero, U.M.M.Z. (1); Rancho Monserrata, U.I.M.N.H. (2), U.M.M.Z. (2); Región Soconusco, U.I.M.N.H. (15); San Bartola, U.I.M.N.H. (12); San Cerónimo, U.I.M.N.H. (1); San Juanito, U.S.N.M. (2); San Ricardo, F.M.N.H. (1); Solosuchiapa, K.U. (2); Tapachula, F.M.N.H. (4), U.I.M.N.H. (3); Tonala, A.M.N.H. (1); F.M.N.H. (2), U.I.M.N.H. (5), U.S.N.M. (1); Tuina, K.U. (1 skeleton); Tuxtla Cutierrez, F.M.N.H. (2); 6 kilometers east of Tuxtla Cutierrez, U.I.M.N.H. (1); 10 kilometers east of Tuxtla Cutierrez, U.M.M.Z. (1). *Chihuahua*: 2.4 kilometers southwest of Toquina, K.U. (2); Riito, K.U. (1). *Coahuila*: mountain near Saltillo, U.I.M.N.H. (2). *Colima*: No specific locality, F.M.N.H. (1); Colima, A.M.N.H. (2); Hacienda Albarradito, U.M.M.Z. (2); Hacienda del Colomo, A.M.N.H. (1); Los Mezcales, U.M.M.Z. (1); Manzanillo, A.M.N.H. (2); Paso del Río, F.M.N.H. (3), U.I.M.N.H. (3), U.M.M.Z. (3); Periquillo, U.M.M.Z. (17); 1.6 kilometers southwest of Pueblo Juárez, U.M.M.Z. (1); Quesaria, F.M.N.H. (4), U.I.M.N.H. (3); U.M.M.Z. (14); Santiago, U.M.M.Z. (1); 7.2 kilometers southwest of Tecolapa, U.M.M.Z. (1). *Guerrero*: Acahuitzotla, U.F. (4); U.M.M.Z. (3); 3 kilometers south of Acahuitzotla, K.U. (5); Acapulco, A.M.N.H. (1), U.M.M.Z. (4), U.S.N.M. (1); 3 kilometers north of Acapulco, U.M.M.Z. (1); 8 kilometers northwest of Acapulco, U.F. (7); 27 kilometers northeast of Acapulco, U.I.M.N.H. (14); Agua del Obispo, F.M.N.H. (5), K.U. (4), U.I.M.N.H. (3); Atoyac, K.U. (4); Buena Vista, F.M.N.H. (4), U.I.M.N.H. (1); Caculutla, K.U. (1); 20 kilometers south of Chilpancingo, F.M.N.H. (5); Colonia Buenas Aires, U.M.M.Z. (1); El Limoncito, F.M.N.H. (4); El Treinte, F.M.N.H. (5), U.I.M.N.H. (3), U.S.N.M.



- (3); Laguna Coyuca, U.M.M.Z. (2); 3 kilometers north of Mazatlán, U.I.M.N.H. (3); 9 kilometers south of Mazatlán, F.M.N.H. (4), U.I.M.N.H. (2); Mexcala, F.M.N.H. (5), U.I.M.N.H. (2); Ocotito, K.U. (10); 5.4 kilometers north of Ocotito, U.M.M.Z. (4); 1.6 kilometers north of Organos, U.I.M.N.H. (12); Palo Blanco, F.M.N.H. (5), U.I.M.N.H. (4); Pie de la Cuesta, A.M.N.H. (5); Puerto Marquez, A.M.N.H. (13); 5.6 kilometers south of San Andreas de la Cruz, K.U. (2); San Vincente, K.U. (1); Zacualpán, U.M.M.Z. (1). *Hidalgo*: below Tianguistengo, F.M.N.H. (1). *Jalisco*: Atenqueque, K.U. (2); 5 kilometers northeast of Autlán, U.I.M.N.H. (1); 5 kilometers east of Barro de Navidad, U.M.M.Z. (1); Charco Hondo, U.M.M.Z. (1); 6.4 kilometers east-northeast of La Huerta, K.U. (2); between La Huerta and Tecomates, K.U. (1); 3 kilometers southeast of La Resolana, K.U. (1, 1 skeleton), 11 kilometers south, 1.6 kilometers east of Yahualica, K.U. (1); Zapotilitic, F.M.N.H. (1). *Michoacán*: Aguililla, U.M.M.Z. (5); Apatzingán, F.M.N.H. (25); K.U. (1 skeleton); 7 kilometers east of Apatzingán, U.M.M.Z. (1); 11 kilometers east of Apatzingán, U.M.M.Z. (3); 27 kilometers south of Apatzingán, K.U. (3); 1.6 kilometers north of Arteaga, U.M.M.Z. (1); Charapendo, U.M.M.Z. (1); Coahuayana, U.M.M.Z. (1); El Sabino, F.M.N.H. (7), U.I.M.N.H. (2); La Placita, U.M.M.Z. (1); La Playa, (1), 30 kilometers east of Nueva Italia, U.M.M.Z. (2); 4 kilometers south of Nueva Italia, U.M.M.Z. (1); Ostula, U.M.M.Z. (4); Salitre de Estopilas, U.M.M.Z. (1); San José de la Montaña, U.M.M.Z. (2); 11 kilometers south of Tumbiscatio, K.U. (1); 12 kilometers south of Tzitzio, U.M.M.Z. (1). *Morelos*: 3.5 kilometers west of Cuautlixco, K.U. (3); Ocotlán del Río, I.P.N. (1), Puente de Ixtla, I.P.N. (1); 1 kilometer northeast of Puente de Ixtla, K.U. (2); 20 kilometers south of Puente de Ixtla, F.M.N.H. (1), U.I.M.N.H. (1); Tequesquitengo, A.M.N.H. (4). *Nayarit*: 3 kilometers south of Acaponeta, U.M.M.Z. (4); 56 kilometers south of Esquinapa (Sinaloa), K.U. (1); Jesús María, A.M.N.H. (1); San Blas, K.U. (5), U.S.N.M. (1); 8.6 kilometers east of San Blas, U.M.M.Z. (1); Tepic, U.I.M.N.H. (4); 4 kilometers east of Tuxpan, K.U. (1); 11 kilometers southeast of Tuxpan, U.I.M.N.H. (28). *Nuevo León*: Caleana, F.M.N.H. (1); Salto Cola de Caballo, F.M.N.H. (63). *Oaxaca*: 11 kilometers south of Candelaria, U.I.M.N.H. (4); Cerro San Pedro, 24 kilometers southwest of Tehuantepec, U.M.M.Z. (1); Chachalapa, K.U. (1); 8 kilometers south of Chiltepec, K.U. (1); 12 kilometers south of Chivela, U.M.M.Z. (1); 12 kilometers south of Chivela, U.M.M.Z. (1); Cocahuatpec, U.I.M.N.H. (1); Coyul, U.S.N.M. (1); 50 kilometers east-southeast of Cuajinicuilapa, U.I.M.N.H. (1); Escurano, U.I.M.N.H. (1); Carza Mora, U.I.M.N.H. (2); Juchatengo, K.U. (1); 17 kilometers northeast of Juchatengo, K.U. (2 tadpoles); Juchitán, U.S.N.M. (1); Lagartero, U.I.M.N.H. (1); Matías Romero, U.I.M.N.H. (1); Mirador, A.M.N.H. (23); Mira León, 1.6 kilometers north of Huatulco, U.I.M.N.H. (2); Mixtequilla, A.M.N.H. (1); Pochutla, K.U. (15), U.I.M.N.H. (9); 17.6 kilometers west-northwest of Puerto Escondido, U.M.M.Z. (1); Quiengola, A.M.N.H. (2); Río del Corte, U.I.M.N.H. (1); Río Mono Blanco, U.I.M.N.H. (1); Río Sarabia, 5 kilometers north of Sarabia, U.M.M.Z. (4); 2.5 kilometers north of Salina Cruz, K.U. (2); San Antonio, U.I.M.N.H. (1); 5 kilometers north-northwest of San Gabriel Mixtepec, K.U. (1); San Pedro del Istmo, U.I.M.N.H. (1); Santo Domingo, U.S.N.M. (3); 3.7 kilometers north of Sarabia, U.M.M.Z. (3); Tapanatepec, K.U. (1, 1 skeleton), U.I.M.N.H. (1), U.M.M.Z. (1); between Tapanatepec and Zanatepec, U.I.M.N.H. (2); Tecuane, U.M.M.Z. (3); Tehuantepec, A.M.N.H. (3), U.M.M.Z. (38), U.S.N.M. (6); 4.5 kilometers west of Tehuantepec, K.U. (14 skeletons); 10 kilometers south of Tehuantepec, K.U. (2); Tehuantepec, K.U. (2); Temazcal, U.S.C. (3); 3 kilometers south of Toluca, K.U. (4); Toluca, A.M.N.H. (1); Tuxtepec, U.M.M.Z. (2), 13 kilometers south of Tuxtepec, U.I.M.N.H. (1); 27 kilometers south of Tuxtepec, U.I.M.N.H. (24); 2 kilometers south of Valle Nacional, K.U. (2); 11 kilometers north of Vista Hermosa, K.U. (1, 6 tadpoles); Yetla, K.U. (1); above Zanatepec, U.I.M.N.H. (1). *Puebla*: 16 kilometers southwest of Mecatepec (Veracruz), U.I.M.N.H. (2); San Diego, A.M.N.H. (1), U.S.N.M. (1); Vegas de Suchil, A.M.N.H. (1); Villa Juárez, U.F. (1). *Quintana Roo*: Cóba, F.M.N.H. (1); Esmeralda, U.M.M.Z. (1); 4 kilometers north-northeast of Felipe Carrillo Puerto, K.U. (2); Pueblo Nuevo X-Can, K.U. (1); 4 kilometers west-southwest of Puerto Juárez, K.U. (5, 1 tadpoles); 12 kilometers west of Puerto Juárez, K.U. (5); San Miguel, Isla de Cozumel, U.M.M.Z. (18); 3.5 kilometers north of San Miguel, Isla de Cozumel, K.U. (4); 10 kilometers east of San Miguel, Isla de Cozumel, U.M.M.Z. (1); Telantunich, F.M.N.H. (1). *San Luis Potosí*: Ciudad Valles, A.M.N.H. (12), F.M.N.H. (2), K.U. (1); 21 kilometers north of Ciudad Valles, U.M.M.Z. (1); 6 kilometers east of Ciudad Valles, U.F. (1); 24 kilometers east of Ciudad Valles, U.F. (5); 5 kilometers south of Ciudad Valles, U.I.M.N.H. (1); 16 kilometers south of Ciudad Valles, A.M.N.H. (1); 30 kilometers south of Ciudad Valles, F.M.N.H. (3), U.I.M.N.H. (2); 63 kilometers south of Ciudad Valles, U.I.M.N.H. (2); Pujal, U.M.M.Z. (2); Río Axtla, near Axtla, A.M.N.H. (6), K.U. (1); Tamazunchale, A.M.N.H. (1), F.M.N.H. (4), U.F. (2), U.I.M.N.H. (1), U.M.M.Z. (11), U.S.N.H. (1); 17 kilometers north of Tamazunchale, U.I.M.N.H. (1); 2.4 kilometers south of Tamazunchale, A.M.N.H. (1); 17 kilometers east of Tamuin, U.F. (2); Xilitla, U.I.M.N.H. (2). *Sinaloa*: 8 kilometers north of Carrizalejo, K.U. (1); 4 kilometers northeast of Concordia, K.U. (1); 5 kilometers southwest of Concordia, K.U. (2); 6 kilometers east of Cosalá, K.U. (1); Costa Rica, 16 kilometers south of Culiacán, U.I.M.N.H. (3); 51 kilometers south-southeast of Culiacán, K.U. (1); El Dorado, K.U. (1); 1.6 kilometers northeast of El Fuerte, F.M.N.H. (1); Isla Palmito del Verde, middle, K.U. (2); 21 kilometers north-northeast of Los Mochis, U.I.M.N.H. (2); Matatán, K.U. (1); 7.3 kilometers southwest of Matatán, K.U. (6); Mazatlán, A.M.N.H. (1), U.M.M.Z. (3); 57 kilometers north of Mazatlán,



U.I.M.N.H. (1); Plomosas, U.S.N.M. (2); Presidio, U.I.M.N.H. (1), U.S.N.M. (1); Rosario, K.U. (2), U.I.M.N.H. (1); 5 kilometers east of Rosario, U.I.M.N.H. (17); 8 kilometers east of Rosario, U.I.M.N.H. (17); 8 kilometers south-south-east of Rosario, K.U. (1); 5 kilometers southwest of San Ignacio, K.U. (1); 1.6 kilometers east-northeast of San Lorenzo, K.U. (8); Teacapán, Isla Palmito del Verde, K.U. (1); 9.6 kilometers north-northwest of Teacapán, K.U. (1); Villa Unión, K.U. (1); 9 kilometers northeast of Villa Unión, K.U. (4); 1 kilometer west of Villa Unión, A.M.N.H. (1). *Sonora*: Cuiracoba, A.M.N.H. (25). *Tabasco*: 4 kilometers northeast of Colmecalco, A.M.N.H. (1); 10 kilometers south of Huimanguillo, U.M.M.Z. (1); Teapa, U.M.M.Z. (1); 5 kilometers north of Teapa, U.M.M.Z. (4); 10 kilometers north of Teapa, U.M.M.Z. (3); 13 kilometers north of Teapa, U.M.M.Z. (7); 21 kilometers north of Teapa, U.M.M.Z. (2); 29 kilometers north of Teapa, U.M.M.Z. (11); Tenosique, U.S.N.M. (3). *Tamaulipas*: Acuña, U.M.M.Z. (1); 5 kilometers south of Acuña, U.M.M.Z. (1); 13 kilometers north of Antiguo Morelos, U.I.M.N.H. (4); 3 kilometers south of Antiguo Morelos, U.F. (1); 3 kilometers northeast of Chamal, U.M.M.Z. (1); 1.6 kilometers east of Chamal, U.M.M.Z. (1); Ciudad Mante, U.M.M.Z. (7); 16 kilometers north of Ciudad Victoria, F.M.N.H. (1); 34 kilometers north of Ciudad Victoria, K.U. (17); 8.8 kilometers south of Ciudad Victoria, U.I.M.N.H. (3); 11 kilometers west of Ciudad Victoria, U.I.M.N.H. (1); 16 kilometers west of Ciudad Victoria, U.I.M.N.H. (1); 3 kilometers west of El Carizo, U.M.M.Z. (1); Cómez Farías, U.M.M.Z. (2); 8 kilometers northeast of Cómez Farías, U.M.M.Z. (18); 8 kilometers northwest of Cómez Farías, U.M.M.Z. (2); 16 kilometers west of Conzales, K.U. (2); Jiménez, K.U. (1); 1.2 kilometers south of La Castilla, U.I.M.N.H. (7); 5 kilometers south of La Castilla, U.I.M.N.H. (23); La Clementina, 6 kilometers west of Forlon, U.S.N.M. (1); Limón, U.I.M.N.H. (1); Llera, U.S.N.M. (4); 3 kilometers east of Llera, U.I.M.N.H. (1); 21 kilometers south of Llera, U.I.M.N.H. (2); 23 kilometers south of Llera, U.I.M.N.H. (1); 11 kilometers southwest of Ocampo, U.M.M.Z. (1); 22 kilometers west, 5 kilometers south of Piedra, K.U. (4); Río Sabinas, U.M.M.Z. (1); 5 kilometers west of San Cerardo, U.M.M.Z. (2); Santa Barbara, U.M.M.Z. (2); Villagran, F.M.N.H. (4), U.I.M.N.H. (2); 1.7 kilometers west of Xicotencatl, U.M.M.Z. (1). *Veracruz*: 1.6 kilometers northwest of Acayucan, U.M.M.Z. (1); 28.5 kilometers southeast of Alvarado, U.M.M.Z. (1); 2.4 kilometers south-southwest of Amatitlán, U.M.M.Z. (1); Azveta, I.P.N. (1); Barranca Metlac, U.I.M.N.H. (1); Boca del Río, U.I.M.N.H. (12), U.M.M.Z. (9); 16 kilometers south of Boca del Río, U.I.M.N.H. (1); between Boca del Río and Antón Lizardo, U.I.M.N.H. (1); Canadá, F.M.N.H. (1); Catemaco, U.M.M.Z. (4); Cerro Chichahuastle, U.I.M.N.H. (1); Ciudad Alemán, U.M.M.Z. (3); Córdoba, F.M.N.H. (3), U.S.N.M. (4); 5.2 kilometers east-southeast of Córdoba, U.M.M.Z. (4); Cosamaloapan, U.M.M.Z. (2); Coyame, U.I.M.N.H. (5), U.M.M.Z. (5); 1 kilometer

southeast of Coyame, U.M.M.Z. (3); Cuatutolapam, U.M.M.Z. (15); Cuautlapan, F.M.N.H. (13), K.U. (22, 9 skeletons), U.I.M.N.H. (78), U.M.M.Z. (38), U.S.N.M. (25); Dos Ríos, F.M.N.H. (1); 5 kilometers east-northeast of El Jobo, K.U. (3); 6.2 kilometers east of Encero, U.I.M.N.H. (1); Escamillo, F.M.N.H. (1), U.I.M.N.H. (1); 1 kilometer north of Fortín de las Flores, U.F. (1); 1 kilometer southwest of Huatusco, U.M.M.Z. (1); 4 kilometers southwest of Huatusco, U.M.M.Z. (1); 10 kilometers southeast of Hueyapan, U.M.M.Z. (1); 20 kilometers south of Jesús Carranza, K.U. (3); 38 kilometers southeast of Jesús Carranza, K.U. (1); Laguna Catemaco, U.M.M.Z. (62); 1.6 kilometers north of La Laja, U.I.M.N.H. (1); La Oaxaqueña, A.M.N.H. (2); 16 kilometers west-southwest of Las Conejos, K.U. (4); 17 kilometers east of Martínez de la Torre, U.I.M.N.H. (3); 6.2 kilometers west of Martínez de la Torre, U.I.M.N.H. (3); 2 kilometers east-northeast of Mata Oscura, K.U. (7); Minatitlán, A.M.N.H. (2); Mirador, U.S.N.M. 6 kilometers south of Monte Blanco, U.F. (4); 21 kilometers east of Nanchital, U.M.M.Z. (1); 2 kilometers south of Naranja, U.M.M.Z. (3); 1.6 kilometers northeast of Novillero, U.M.M.Z. (2); 3 kilometers northeast of Novillero, U.M.M.Z. (1); 5.2 kilometers northeast of Novillero, U.M.M.Z. (4); 6 kilometers northeast of Novillero, U.M.M.Z. (1); 5 kilometers north of Nueva Colonia, U.M.M.Z. (1); Orizaba, U.S.N.M. (2); 4 kilometers northeast of Orizaba, U.M.M.Z. (2); Otatitlán, U.I.M.N.H. (17); 10 kilometers west-southwest of Pachuquillo, K.U. (5); Panuco, U.M.M.Z. (1); Paraje Nuevo, U.M.M.Z. (73); Paso del Macho, U.I.M.N.H. (1); Paso de Talayo, Jicaltepec, U.S.N.M. (2); Pérez, F.M.N.H. (5); 20 kilometers north of Piedras Negras, Río Blanco, K.U. (1); Plan del Río, K.U. (6), U.M.M.Z. (6); Potrero, U.I.M.N.H. (4), U.M.M.Z. (4), U.S.N.M. (5); Potrero Viejo, F.M.N.H. (1), K.U. (40, 4 skeletons), U.I.M.N.H. (1), U.M.M.Z. (27), U.S.N.M. (10), 5 kilometers south of Potrero Viejo, K.U. (3); Puente Nacional, U.I.M.N.H. (6); 3 kilometers north of Rinconada, U.M.M.Z. (5); Río de las Playas, U.S.N.M. (2); Río Seco, U.M.M.Z. (9); Rodríguez Clara, F.M.N.H. (1); San Andrés Tuxtla, F.M.N.H. (4), U.I.M.N.H. (3); 5 kilometers north of San Andrés Tuxtla, U.I.M.N.H. (1); 10 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (1); 13.4 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (2); 19.8 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (1); 27.2 kilometers northwest of San Andrés Tuxtla, U.M.M.Z. (1); 4 kilometers west of San Andrés Tuxtla, U.M.M.Z. (1); 37.4 kilometers south of San Andrés Tuxtla, U.M.M.Z. (12); 15 kilometers east-southeast of San Juan de la Punta, K.U. (1); San Lorenzo, U.S.N.M. (5); 3 kilometers southwest of San Marcias, K.U. (1); 1.5 kilometers south of Santa Rosa, U.I.M.N.H. (1); 2 kilometers south of Santiago Tuxtla, U.M.M.Z. (4); Suazel, U.M.M.Z. (1); 14 kilometers east of Suchil, U.I.M.N.H. (1); 15 kilometers south of Tampico (Tamaulipas), U.M.M.Z. (4); 4 kilometers north of Tapalapan, U.M.M.Z. (2); Tecolutla, U.I.M.N.H. (24); 16 kilometers northwest

of Tehuatlán, U.I.M.N.H. (4); 5 kilometers south of Tehuatlán, K.U. (1); Teocelo, K.U. (1); Tierra Colorada, F.M.N.H. (3), U.I.M.N.H. (3); Veracruz, A.M.N.H. (9), I.P.N. (1), U.I.M.N.H. (1), U.M.M.Z. (3); 24 kilometers west of Veracruz, F.M.N.H. (3). *Yucatán*: No specific locality, F.M.N.H. (2), U.S.N.M. (1); Chichén-Itzá, F.M.N.H. (17), U.I.M.N.H. (5), U.M.M.Z. (73), U.S.N.M. (1); 9 kilometers east of Chichén-Itzá, K.U. (2); 12 kilometers east of Chichén-Itzá, K.U. (1); Mérida, F.M.N.H. (8), U.I.M.N.H. (2), U.M.M.Z. (1); 6 kilometers south of Mérida, K.U. (1); 8.8 kilometers southeast of Ticul, U.M.M.Z. (1); Valladolid, F.M.N.H. (3); Xcalah-op, F.M.N.H. (9); 3.5 kilometers east of Yokdzonot, K.U. (3, 1 tadpoles).

**BRITISH HONDURAS:** *Belize*: Belize, F.M.N.H. (4), U.M.M.Z. (1), U.S.N.M. (1); Manatee, F.M.N.H. (4). *Cayo*: Cayo, U.M.M.Z. (1); 6 kilometers south of Cayo, M.C.Z. (1); 2.5 kilometers southwest of Cayo, U.M.M.Z. (1); Cocquericot, U.M.M.Z. (2); Cohune Ridge, U.M.M.Z. (15); Double Falls, F.M.N.H. (1); Mountain Pine Ridge, M.C.Z. (2); Pine Ridge Road, U.M.M.Z. (18); San Augustin, U.M.M.Z. (1); Valentin, U.M.M.Z. (8). *Orange Walk*: Gallon Jug, M.C.Z. (8). *Stann Creek*: Bokowina, F.M.N.H. (2); Hummingbird Highway between Roaring Creek and Stann Creek, U.M.M.Z. (1); 16 kilometers from Hummingbird Highway on road to Monkey River, U.M.M.Z. (1); 5 kilometers south of Waha Loaf Creek, M.C.Z. (1). *Toledo*: San Pedro Colombia, M.C.Z. (3).

**GUATEMALA:** *Alta Verapaz*: 5.1 kilometers northeast of Campur, K.U. (2 tadpoles); 28.3 kilometers northeast of Campur, K.U. (20, 2 skeletons); Chamá, M.C.Z. (2), U.M.M.Z. (56); Chinajá, K.U. (8, 1 eggs, 3 tadpoles); Cobán, F.M.N.H. (1); Cubilquitz, U.M.M.Z. (10); Finca Canihor, U.M.M.Z. (1); Finca Chicoyou, K.U. (4, 3 tadpoles); Finca Los Alpes, K.U. (5, 1 tadpoles); Finca Los Pinales, U.M.M.Z. (2); Finca Tinajas, B.Y.U. (1); Finca Volcán, U.M.M.Z. (6); Panzós, M.N.H.N. (1), U.M.M.Z. (1); Samac, U.M.M.Z. (1); Samanzana, U.M.M.Z. (6). *Baja Verapaz*: Chejel, U.M.M.Z. (10); San Gerónimo, U.M.M.Z. (16). *Chiquimula*: 1.6 kilometers southeast of Chiquimula, U.M.M.Z. (1); Esquipulas, U.M.M.Z. (28). *El Petén*: Asceradero Machaquila, U.M.M.Z. (1); 20 kilometers north-northwest of Chinajá (Alta Verapaz), K.U. (42); Flores, U.M.M.Z. (1); La Libertad, K.U. (1 tadpoles); U.M.M.Z. (57); 3 kilometers southeast of La Libertad, K.U. (2); 13 kilometers south of La Libertad, M.C.Z. (2); Pacomon, U.S.N.M. (1); Piedras Negras, U.S.N.M. (3); Poptún, U.M.M.Z. (3); Pozo de la Jicotea, U.S.N.M. (1); Ramate-Yaxha trail, U.M.M.Z. (1); Río de la Pasión between Sayaxché and Subín, K.U. (1); Río San Román, 16 kilometers north-northwest of Chinajá (Alta Verapaz), K.U. (5); Sachuc, U.S.N.M. (1); Sayaxché, K.U. (2); Tikal, U.M.M.Z. (22); Toocog, K.U. (2, 2 tadpoles); Uaxactún, U.M.M.Z. (3); Yaxha, U.M.M.Z. (1); 19 kilometers east of Yaxha, U.M.M.Z. (4). *El Quiché*: Finca Tesoro, U.M.M.Z. (3, 1 tadpoles). *Escuintla*: Río

Guacalate, Masagua, U.S.N.M. (1); Tiquisate, U.M.M.Z. (7). *Guatemala*: 16 kilometers northeast of Guatemala, K.U. (9). *Huehuetenango*: Barillas, U.M.M.Z. (2); Cuilco, U.M.M.Z. (12); Finca San Rafael, 16 kilometers southeast of Barillas, F.M.N.H. (5); 45 kilometers west-northwest of Huehuetenango, K.U. (2); Jacaltenango, U.M.M.Z. (33); La Democracia, U.M.M.Z. (8). *Izabál*: 2 kilometers southwest of Puerto Matías de Gálvez, K.U. (2 tadpoles); Quirigua, F.M.N.H. (1), U.M.M.Z. (1). *Jalapa*: Jalapa, U.M.M.Z. (12). *Jutiapa*: Finca La Trinidad, U.M.M.Z. (10); Jutiapa, U.M.M.Z. (1); 1.6 kilometers southeast of Mongoy, K.U. (1); Santa Catarina Mita, U.M.M.Z. (1). *Progreso*: Finca Los Leones, U.M.M.Z. (1). *Quetzaltenango*: Coatepeque, A.M.N.H. (1). *Retalhuleu*: Casa Blanca, U.M.M.Z. (18); Champerico, U.M.M.Z. (3). *San Marcos*: Puente Talismán, U.S.N.M. (2). *Santa Rosa*: Finca La Guardiania, U.M.M.Z. (6); Finca La Gloria, U.M.M.Z. (6); 1.6 kilometers west-southwest of El Molino, K.U. (4). *Suchitepequez*: Mazatenango, U.I.M.N.H. (1).

**EL SALVADOR:** *La Libertad*: 16 kilometers northwest of Santa Tecla, K.U. (3). *Morazán*: Divisadero, U.S.N.M. (1). *San Salvador*: San Salvador, F.M.N.H. (13), K.U. (34, 2 skeletons, 1 eggs, 7 tadpoles), U.M.M.Z. (6), U.S.N.M. (1).

**HONDURAS:** *Atlantida*: Isla de Roatán, F.M.N.H. (4); La Ceiba, U.S.N.M. (4); Lancetilla, M.C.Z. (5); Tela, M.C.Z. (3), U.M.M.Z. (1), U.S.N.M. (2). *Choluteca*: 1.5 kilometers northwest of Choluteca, K.U. (5); 10 kilometers northwest of Choluteca, K.U. (1); 10 kilometers east of Choluteca, K.U. (2); 12 kilometers east of Choluteca, K.U. (1); 5 kilometers south of Choluteca, U.S.C. (2). *Colón*: Balfate, A.M.N.H. (4); Bambú, U.F. (1); Patuca, U.S.N.M. (1); Río Segovia, M.C.Z. (1). *Comayagua*: La Misión, 3.5 leagues north of Signatepeque, M.C.Z. (2). *Copán*: Copán, U.M.M.Z. (2). *Cortés*: Cofradía, A.M.N.H. (2); Hacienda Santa Ana, F.M.N.H. (8); Lago de Yojoa, M.C.Z. (2); Río Lindo, A.M.N.H. (1); San Pedro Su'a, K.U. (1). *El Paraíso*: El Volcán, M.C.Z. (1). *Francisco Morazán*: Guaimaca, U.M.M.Z. (1); Tegucigalpa, B.Y.U. (9), M.C.Z. (3), U.S.N.M. (1). *Santa Barbara*: Santa Barbara, U.S.N.M. (4).

**NICARAGUA:** *Carazo*: 3 kilometers north, 4 kilometers west of Ciriamba, K.U. (5). *Chinandega*: 4 kilometers north, 2 kilometers west of Chichigalpa, K.U. (1); Chinandega, M.C.Z. (1); Hacienda Bellavista, Volcán Casita, K.U. (4); Río Tama, U.S.N.M. (1); San Antonio, K.U. (20, 6 skeletons). *Chontales*: 1 kilometer northeast of Acoyapa, K.U. (1); 1 kilometer north, 2.5 kilometers west of Villa Somoza, K.U. (1). *Estelí*: Finca Daraili, 5 kilometers north, 15 kilometers east of Condega, K.U. (5); Finca Venecia, 7 kilometers north, 16 kilometers east of Condega, K.U. (1). *León*: 1.6 kilometers east-northeast of PoneLOYA, K.U. (2). *Managua*: Managua, U.S.N.M. (2); 8 kilometers northwest of Managua, K.U. (17); 20 kilometers northeast of Managua, K.U. (3); 5 kilometers southwest of Managua, K.U. (8); 1-3 kilo-



meters north of Sabana Grande, K.U. (14); 20 kilometers south of Tipitapa, K.U. (1). *Matagalpa*: Guasqualie, U.M.M.Z. (1); Matagalpa, U.M.M.Z. (1); 19 kilometers north of Matagalpa, U.M.M.Z. (1); Sébaeo, K.U. (1). *Nueva Segovia*: 1.5 kilometers north, 1 kilometer east of Jalapa, K.U. (8); 5 kilometers north, 2.5 kilometers east of Jalapa, K.U. (6). *Río San Juan*: Greytown, U.S.N.M. (4). *Rivas*: Javillo, U.M.M.Z. (1); Moyogalpa, Isla Ometepe, K.U. (10, 1 tadpoles); Peñas Blancas, K.U. (1); Río Javillo, 3 kilometers north, 4 kilometers west of Sapoá, K.U. (3, 1 skeleton); 13.1 kilometers southeast of Rivas, K.U. (1); 14.8 kilometers southeast of Rivas, K.U. (3); 11 kilometers south, 3 kilometers east of Rivas, K.U. (1); 16 kilometers south of Rivas, M.C.Z. (2); 7.7 kilometers northeast of San Juan del Sur, K.U. (2); 16.5 kilometers northeast of San Juan del Sur, K.U. (2, 1 tadpoles); 5 kilometers southeast of San Pablo, K.U. (5). *Zelaya*: Bonanza, K.U. (2); Cooley, A.M.N.H. (11); Cukra, A.M.N.H. (2); El Reereo K.U. (10); Masahuas, Río Huaspue, A.M.N.H. (4); 11 kilometers northwest of Rama, Río Siquia, U.M.M.Z. (8); Río Escondido, U.S.N.M. (2); Río Siquia at Río Mico, U.M.M.Z. (10); Sioux Plantation, A.M.N.H. (15).

**COSTA RICA:** *Alajuela*: Los Chiles, A.M.N.H. (1); Orotina, M.C.Z. (2); San Carlos, U.S.N.M. (1). *Guanacaste*: Finca Taboga, K.U. (5); La Cruz, U.S.Z. (3); 4.3 kilometers northeast of La Cruz, U.S.N.M. (1); 18.4 kilometers south of La Cruz, U.S.C. (1); 23.5 kilometers south of La Cruz, U.S.C. (4); 3 kilometers west of La Cruz, U.S.C. (4); 2 kilometers northeast of Las Cañas, K.U. (3); Las Huecas, U.M.M.Z. (2); Liberia, K.U. (1), U.S.C. (1); 11.5 kilometers north of Liberia, U.S.C. (1); 13 kilometers north of Liberia, U.S.C. (1); 22.4 kilometers north of Liberia, U.S.C. (1); 8 kilometers north-northwest of Liberia, K.U. (1); Peñas Blancas, K.U. (2); 8.6 kilometers east-southeast of Playa del Coco, U.S.C. (1); 2.8 kilometers east-southeast of Playa del Coco, U.S.C. (1); Río Piedra, 1.6 kilometers west of Bagaces, U.S.C. (1); Río Bebedero, 5 kilometers south of Bebedero, K.U. (1); 5 kilometers northeast of Tilarán, K.U. (5). *Heredia*: Puerto Viejo, K.U. (4); 13 kilometers southwest of Puerto Viejo, K.U. (5). *Limón*: Batán, K.U. (1); Cuacimo, U.S.C. (1); Los Diamantes, K.U. (1); Pandora, U.S.C. (3); Suretka, K.U. (2); Tortugero, U.F. (4). *Puntarenas*: Barranca, F.M.N.H. (3); 15 kilometers west-northwest of Barranca, K.U. (3), U.M.M.Z. (1); 18 kilometers west-northwest of Barranca, U.M.M.Z. (4); 4 kilometers west-northwest of Esparta, K.U. (38, 5 skeletons); 19 kilometers northwest of Esparta, K.U. (8).

#### *Smilisea cyanostieta*

**MEXICO:** *Chiapas*: Monte Libano, M.C.Z. (9); 8 kilometers north of San Fernando, 24 kilometers east of Tuxtla Gutierrez, U.I.M.N.H. (1). *Oaxaca*: 11 kilometers north of Campamento Vista Hermosa, K.U. (15, 3 skeletons, 1 eggs, 6 tadpoles), U.I.M.N.H. (3), 8 kilometers south of Yetla, K.U. (1); U.M.M.Z.

(8). *Veracruz*: Coyame, U.M.M.Z. (2); between Coyame and Tebanco, U.M.M.Z. (1); Dos Amates, U.M.M.Z. (1); between Laguna de Catemaco and Voleán San Martín, U.M.M.Z. (1); Voleán San Martín, U.I.M.N.H. (7), U.M.M.Z. (6).

**CUATEMALA:** *Alta Verapaz*: Chinajá, K.U. (3, 1 skeleton). *El Petén*: 10 kilometers north-northwest of Chinajá (Alta Verapaz), K.U. (1); Piedras Negras, F.M.N.H. (3), U.I.M.N.H. (1), U.S.N.M. (8); 8 kilometers south of Piedras Negras, F.M.N.H. (1); Semicoch, U.S.N.M. (1).

#### *Smilisea phacota*

**NICARAGUA:** *Matagalpa*: Finca Tepeyac, 10 kilometers north, 9 kilometers east of Matagalpa, K.U. (1, 1 tadpoles); Matagalpa, M.C.Z. (2), U.M.M.Z. (1); 19 kilometers north of Matagalpa, U.M.M.Z. (2); Santa María de Ostuma, K.U. (1). *Zelaya*: Bonanza, K.U. (31, 3 skeletons, 2 tadpoles); Cukra, A.M.N.H. (1); El Reereo, K.U. (62); Río Mico, 16 kilometers east of Reereo, U.M.M.Z. (10); junction of Río Mico and Siguia, U.M.M.Z. (10); Río Siguia, 11 kilometers northwest of Rama, U.M.M.Z. (49).

**COSTA RICA:** *Alajuela*: Cinchona, K.U. (4); 5 kilometers south of Ciudad Quesada, U.S.C. (1); Laguna Monte Alegre, K.U. (2); Las Playuelas, 11 kilometers south of Los Chiles, U.S.C. (1); San Carlos, U.S.N.M. (1). *Cartago*: Moravia de Turrialba, K.U. (41, 1 skeleton), U.S.C. (3); Peralta, K.U. (2); Río Chitara, 3 kilometers north-northeast of Pavones, K.U. (7, 1 eggs, 7 tadpoles); Río Reventazón, M.C.Z. (8), U.M.M.Z. (9); Turrialba, K.U. (46, 3 skeletons), M.C.Z. (3, 1 tadpoles), U.S.N.M. (1). *Guanacaste*: Tilarán, K.U. (3); 8 kilometers northeast of Tilarán, K.U. (2). *Heredia*: Barranca del Río Sarapiquí below Isla Bonita, K.U. (2); Cariblanco, K.U. (6, 1 skeleton), M.C.Z. (1); Isla Bonita, K.U. (5); Puerto Viejo, K.U. (1); 4.2 kilometers west of Puerto Viejo, K.U. (2); 7.5 kilometers west of Puerto Viejo, K.U. (1). *Limón*: Bambú, U.S.C. (4); Batán, U.M.M.Z. (1); Coén, M.C.Z. (1); La Lola, K.U. (3), U.F. (1), M.C.Z. (3); Los Diamantes, F.M.N.H. (4), K.U. (6); Pandora, U.M.M.Z. (2); U.S.C. (4); Puerto Limón, K.U. (1); Río Lari at Río Dipari, 21 kilometers southwest of Amubre, U.S.C. (1); Río Toro Amarillo, 7 kilometers west of Guálpes, K.U. (1, 1 tadpoles); Suretka, K.U. (4). *Puntarenas*: Agua Buena, K.U. (1); 1.6 kilometers east of Buenos Aires, U.M.M.Z. (1); 3 kilometers northwest of Buenos Aires, K.U. (1); 4 kilometers north, 15 kilometers west of Dominical, K.U. (2 tadpoles); Esparta, M.C.Z. (3); Colfito, K.U. (1); 6 kilometers east of Colfito, K.U. (2 skeletons); Gromaco, U.M.M.Z. (4); Palmar, K.U. (1); 4 kilometers east-southeast of Palmar Sur, K.U. (2); 5.6 kilometers southeast of Palmar Sur, K.U. (1 tadpoles); 7.0 kilometers southeast of Palmar Sur, K.U. (1 tadpoles); 8.5 kilometers southeast of Piedras Blancas, K.U. (12); Quebrada Boruea, 22 kilometers east of Palmar Norte, K.U. (1); Rincón de Osa, K.U. (15, 2 tadpoles), U.M.M.Z. (3), U.S.C. (1); Río Ferruviosa, 7 kilometers south of Rincón de Osa, U.S.C. (1); 1.6 kilometers west-



northwest of Villa Neily, K.U. (2 tadpoles). *San José*: San Isidro el General, K.U. (1), U.M.M.Z. (1); 10 kilometers north of San Isidro el General, M.C.Z. (5); 13 kilometers west-southwest of San Isidro el General, K.U. (1); 15 kilometers west-southwest of San Isidro el General, K.U. (3 tadpoles); 20 kilometers west-southwest of San Isidro el General, K.U. (1).

PANAMA: *Bocas del Toro*: Almirante, K.U. (3); 1.6 kilometers west of Almirante, K.U. (1); 3 kilometers west of Almirante (10, 1 skeleton), 11 kilometers northwest of Almirante, F.M.N.H. (9); 13 kilometers west of Almirante, K.U. (6, 3 skeletons); Fish Creek, K.U. (1); Isla Popa, K.U. (2); mouth of Río Cahuita, K.U. (1); Río Changena, 650 meters, K.U. (2); Río Changena, 830 meters, K.U. (8). *Canal Zone*: Barro Colorado Island, F.M.N.H. (9), M.C.Z. (5), U.F. (1), U.M.M.Z. (18); 3.7 kilometers west of Cocolí, K.U. (1); Fort Sherman, M.C.Z. (1); Catún, M.C.Z. (1); junction roads C25B and C16, T.N.H.C. (1); Madden Forest, K.U. (1), T.N.H.C. (2); Río Agua Salud, 13 kilometers northwest of Camboa, K.U. (5). *Chiriquí*: 2 kilometers west of Concepción, A.M.N.H. (1); Progreso, U.M.M.Z. (5). *Coclé*: El Valle, K.U. (4, 1 tadpoles), T.N.H.C. (1). *Colón*: Achioté, K.U. (5, 1 tadpoles); Quipo, A.M.N.H. (2); Río Candelaria, F.M.N.H. (2). *Darien*: Camp Creek, Camp Townsend, A.M.N.H. (3); Cana, K.U. (1), U.S.N.M. (1); Río Chucunaque, 7 kilometers above Río Mortí, K.U. (2); Río Esnape, Sambú Valley, M.C.Z. (1); Río Subcutí, Chanchiman's Creek, A.M.N.H. (1); Río Tuira at Río Mono, K.U. (1). *Panamá*: northwest slope of Cerro Prominente, K.U. (1); Finca La Sumbadora, K.U. (1 skeleton). *San Blas*: Armila, U.S.N.M. (1); Sasardi, K.U. (4). *Veraguas*: mouth of Río Concepción, K.U. (1).

#### *Smilisca puma*

NICARAGUA: No specific locality, U.S.N.M. (1).

COSTA RICA: *Alajuela*: Jabillos, 5 kilometers north of Santa Clara, U.S.C. (6); 5 kilometers west of La Fortuna, U.S.C. (2); Río La Fortuna at La Fortuna, U.S.C. (3). *Cartago*: Laguna Bonilla, tunnel camp near Peralta, K.U. (1). *Heredia*: Puerto Viejo, K.U. (2), M.C.Z. (2); 5.9 kilometers west of Puerto Viejo, K.U. (1); 7.5 kilometers west of Puerto Viejo, K.U. (18, 7 skeletons, 2 tadpoles). *Limón*: Batán, K.U. (3); La Losa, K.U. (1), U.S.C. (3); Los Diamantes, K.U. (1), U.M.M.Z. (6), U.S.C. (1); 2.4 kilometers east of Los Diamantes, U.S.C. (5).

#### *Smilisca sila*

COSTA RICA: *Puntarenas*: 6 kilometers east of Colfíto, K.U. (1); Quebrada Boruca, 22 kilometers east of Palmar Norte, K.U. (2); Río Zapote, 8 kilometers east of Palmar Norte, U.S.C. (2). *San José*: San Isidro el General, K.U. (1); 14 kilometers northwest of San Isidro el General, U.S.C. (2); 15 kilometers west-southwest of San Isidro el General, U.S.C. (1).

PANAMA: *Canal Zone*: Barro Colorado Island, A.M.N.H. (4), F.M.N.H. (10), K.U. (7, 1 skeleton, 1 tadpoles), U.M.M.Z. (5), U.S.C. (1). *Chiriquí*: Boquete, A.M.N.H. (1), U.M.M.Z. (5); El Volcán, K.U. (24, 4 skeletons, 1 eggs, 1 tadpoles); 6 kilometers south of El Volcán, F.M.N.H. (1); 16 kilometers north-northwest of El Volcán, K.U. (12); Finca Palo-santo, 6 kilometers west-northwest of El Volcán, K.U. (12, 1 skeleton); Finca Santa Clara, K.U. (1); Río Colorado, 17 kilometers north-northwest of El Volcán, K.U. (2); Valle Hornito, 19 kilometers northeast of Gualaca, K.U. (13). *Coclé*: El Valle, A.M.N.H. (21), F.M.N.H. (20), K.U. (3, 1 tadpoles), T.N.H.C. (2), U.S.N.M. (1). *Darién*: Camp Creek, Camp Townsend, A.M.N.H. (7); Río Chico, A.M.N.H. (3); Río Pita, F.M.N.H. (3); Tacarcuna, U.S.N.M. (7); Three Falls Creek, A.M.N.H. (2). *Los Santos*: Cerro Corbatal, K.U. (9); Cerro Hoya, K.U. (5, 2 tadpoles), U.S.N.M. (2); Cuanico Arriba, Río Cuánico, K.U. (3, 1 tadpoles); Lajamina, Río Puira, K.U. (1). *Panamá*: Altos de Pacora, K.U. (1); Cerro Jefe, K.U. (2); Cerro La Campana, F.M.N.H. (1), K.U. (5), U.S.N.M. (1); Finca La Sumbadora, K.U. (15, 2 skeletons, 1 eggs, 4 tadpoles); Río Calobra, U.S.N.M. (1); Río Pacora, 9 kilometers north-northeast of Pacora, K.U. (1). *San Blas*: Sasardi, K.U. (17, 5 skeletons). *Veraguas*: Cerro Carbuco, U.S.N.M. (1); Cerro Tute, F.M.N.H. (5); Isla Cebaco, Río Platanal, K.U. (3).

#### *Smilisca sordida*

NICARAGUA: *Zelaya*: Río Crande, M.C.Z. (1).

COSTA RICA: *Alajuela*: between Atena and Salto de San Mateo, U.S.C. (1); 8 kilometers north of Ciudad Quesada, U.S.C. (4); La Fortuna, U.S.C. (20); 3 kilometers east of La Fortuna, U.S.C. (1); San Carlos, U.S.N.M. (1); Sarchi, K.U. (12). *Cartago*: Cartago, B.M.N.H. (1); headwaters of Río Pacuare, U.S.C. (1); 10 kilometers north of Río Reventazon bridge, U.S.C. (1); 5 kilometers southwest of Río Reventazon bridge on Paraiso-Orosi road, U.S.C. (1); Turrialba, K.U. (1), M.C.Z. (1), U.M.M.Z. (1), U.S.C. (3), U.S.N.M. (4). *Heredia*: Puerto Viejo, K.U. (1); 5 kilometers west of Puerto Viejo, T.C.W.C. (15). *Guanacaste*: Las Cañas, U.S.C. (1); Santa Cecilia, M.C.Z. (2); Tilarán, U.S.C. (5). *Limón*: Bambú, U.S.C. (15); La Lola, U.S.C. (10); Pandora, U.S.C. (16); Pico Blanco, U.S.N.M. (2); Río Lari, 14-16 kilometers southwest of Annubre, U.S.C. (11); Sipurio, U.S.N.M. (2); Suretka, K.U. (14, 1 skeleton). *Puntarenas*: 6 kilometers north of Dominical, K.U. (2, 2 tadpoles); Esparta, M.C.Z. (1); 6 kilometers east of Colfíto, K.U. (24, 4 skeletons, 2 tadpoles), U.S.C. (23); Quebrada Auga Buena, 3 kilometers southwest of Rincón de Osa, U.S.C. (6); Quebrada Boruca, 22 kilometers east of Palmar Norte, K.U. (1); Rincón de Osa, K.U. (44, 3 tadpoles), U.M.M.Z. (6, 1 skeleton), U.S.C. (7); Río Barranca, U.S.C. (2); Río Ceiba, 6 kilometers northwest of Buenos Aires, K.U. (2), U.S.C. (7); Río Ciruelitas, 16 kilometers north-west of Esparta, U.S.C. (3); Río Claro, 14.2 kilo-

meters northwest of Villa Neily, U.S.C. (4); Río Ferruviosa, 7 kilometers south of Rincón de Osa, U.S.C. (4); Río Lagarto at Pan-American Highway (Guanacaste border), U.S.C. (4); Río La Vieja, 30 kilometers east of Palmar Norte, K.U. (4, 1 tadpoles), U.S.C. (2); Río Oro, 28.5 kilometers northwest of Villa Neily, K.U. (1); Río Volcán, 10 kilometers west of Buenos Aires, U.S.C. (1); Río Zapote, 8 kilometers east of Palmar Norte, U.S.C. (4); 3-5 kilometers west of Palmar, U.S.C. (18); 7 kilometers southeast of Palmar Sur, K.U. (3); 1-5 kilometers northwest of Villa Neily, U.S.C. (23). *San José*: Bajos de Jorco, K.U. (1 tadpoles); Escazu, K.U. (8), U.S.C. (1); Paso Ancho, Río Jorco, U.M.M.Z. (6), U.S.C. (3); Río Jorco, near Desamparados, K.U. (11, 4 skeletons), U.S.C. (9); Río Peje, 10 kilometers south-southeast of San Isidro el General, U.S.C. 7115, (3); Río Tiriví, M.C.Z. (1); San Isidro el General, F.M.N.H. (1), K.U. (2), U.M.M.Z. (1); 15 kilometers west-southwest of San Isidro el General, K.U. (19, 3 tadpoles), U.S.C. (6); 17.1 kilometers west-southwest of San Isidro el General, U.S.C. (1); 18 kilometers west-southwest of San Isidro el General, U.S.C. (1); 20 kilometers west-southwest of San Isidro el General, K.U. (6, 3 skeletons, 6 tadpoles); San José, A.M.N.H. (4), U.S.C. (1); Santa Rosa, U.S.C. (3).

PANAMA: *Chiriquí*: Río Jacu, 5.8 kilometers east-southeast of Paso Canoas, K.U. (1). *Veraguas*: No specific locality, Z.M.B. (2).

#### *Tripriorion petasatus*

MEXICO: *Campeche*: 5 kilometers south of Champotón, K.U. (1); Dzibichén, K.U. (14); 7.5 kilometers west of Escárcega, K.U. (4). *Quintana Roo*: 6.5 kilometers south of Las Palmas, 57 kilometers south of Felipe Carrillo Puerto, U.I.M.N.H. (4). *Yucatán*: Cenote Tamanché, U.S.N.M. (1); Chichén Itzá, F.M.N.H. (3), U.M.M.Z. (76); 2.5 kilometers east of Chichén Itzá, K.U. (11, 1 skeleton); 9 kilometers east of Chichén Itzá, K.U. (17, 2 tadpoles); 12 kilometers east of Chichén Itzá, K.U. (19, 3 skeletons, 1 tadpoles); Dzibichaltun, K.U. (4); 6 kilometers south of Mérida, K.U. (1 tadpoles); 7 kilometers north of Muna, K.U. (1); Pisté, (2, 2 skeletons); 3.5 kilometers north of Pisté, K.U. (1 tadpoles); Santa Elena, 4.8 kilometers south of Talcha, U.M.M.Z. (1); Tekom, F.M.N.H. (14); 8.8 kilometers southeast of Ticul, U.M.M.Z. (1); 3.5 kilometers east of Yokdzonot, K.U. (35, 2 skeletons, 4 eggs, 2 tadpoles).

GUATEMALA: *El Petén*: La Libertad, F.M.N.H. (2), S.U. (1), U.M.M.Z. (34, 1 skeleton); Tikal, U.F. (8).

#### *Tripriorion spatulatus reticulatus*

MEXICO: *Colima*: 10.5 kilometers south of Colima, U.I.M.N.H. (67); 19.5 kilometers south of Colima, U.I.M.N.H. (3); 21 kilometers south of Colima, K.U. (3), T.N.H.C. (5); 5.6 kilometers north of Los Asmoles, A.M.N.H. (2); 22.2 kilometers east of Manzanillo, U.I.M.N.H. (27); Santiaguito, 11 kilometers north of Colima, U.I.M.N.H. (196); 10.9 kilometers north of Santiaguito, U.I.M.N.H. (12); Tecolapa, U.I.M.N.H. (10). *Guerrero*: 5 kilometers east of El Zapote, K.U. (31, 6 skeletons). *Michoacán*: Ostula, U.M.M.Z. (8); between Río Marquez and Cuatro Caminos, K.U. (3). *Oaxaca*: Cerro Arenal, U.S.N.M. (1); Cerro San Pedro, U.I.M.N.H. (1); Chivela, A.M.N.H. (1), M.C.Z. (1); Garza Mora, U.I.M.N.H. (1); 2.4 kilometers north of Salina Cruz, K.U. (1, 1 skeleton), U.M.M.Z. (26, 2 skeletons, 2 tadpoles); San Antonio, near Tehuantepec, C.A.S. (1), T.C.W.C. (1), U.I.M.N.H. (3); Tehuantepec, U.I.M.N.H. (2); 8.6 kilometers west of Tehuantepec, K.U. (1), U.M.M.Z. (11, 2 skeletons).

#### *Tripriorion spatulatus spatulatus*

MEXICO: *Sinaloa*: 4 kilometers northeast of Concordia, K.U. (2); 3 kilometers east of Concordia, L.B.S.C. (7, 1 skeleton), 5 kilometers southwest of Concordia, K.U. (8); 8 kilometers southwest of Concordia, K.U. (4); 88 kilometers south of Culiacán, K.U. (4, 3 skeletons); 36.5 kilometers south of El Salado, U.I.M.N.H. (1); 10 kilometers northeast of La Cruz, L.A.C.M. (51); Mazatlán, K.U. (1), M.C.Z. (1, 1 skeleton); 6.6 kilometers north of Mazatlán, L.B.S.C. (1); 11 kilometers north of Mazatlán, L.B.S.C. (1 skeleton); 13 kilometers north of Mazatlán, L.B.S.C. (1); 14.4 kilometers north of Mazatlán, A.M.N.H. (1); 25 kilometers north of Mazatlán, L.B.S.C. (2); 31 kilometers north-northwest of Mazatlán, A.M.N.H. (1 skeleton), K.U. (1 skeleton), U.M.M.Z. (15); road to San Ignacio, L.A.C.M. (6); Venadillo, U.S.N.M. (1); 9.1 kilometers northeast of Villa Unión, K.U. (9); 15.4 kilometers northeast of Villa Unión, L.A.C.M. (1); 21 kilometers southeast of Villa Unión, L.A.C.M. (1); 26 kilometers south-east of Villa Unión, L.A.C.M. (1).

## APPENDIX 2

The data for the specimens, recordings, and photographs comprising the illustrations on plates 1-72 are given below.

### PLATE 1.

1. *Hyla zeteki*, K.U. No. 36481, La. Palma, San José Province, Costa Rica. 2. *Hyla mixe*, K.U. No. 87100, 4.2 kilometers south of Campamento Vista Hermosa, Oaxaca, México. 3. *Hyla regilla curta*, K.U. No. 78370, Todos Santos, Baja California Sur, México.

### PLATE 2.

1. *Pterohyla dentata*, K.U. No. 60083, 15 kilometers east of Aguascalientes, Aguascalientes, México. 2. *Hyla cehinata*, U.M.M.Z. No. 123987, Campamento Vista Hermosa, Oaxaca, México. 3. *Hyla valanceifer*, K.U. No. 95416, Volcán San Martín, Veracruz, México.

### PLATE 3.

1. *Hyla fimbrimembra*, R.C.T. No. 761, Cinchona, Alajuela, Costa Rica. 2. *Hyla thysanota*, U.S.N.M. No. 151080, Cerro Malí, Darién Province, Panamá.

### PLATE 4.

1. *Hyla pachyderma*, U.S.N.M. No. 115026, Pan de Olla, Veracruz, México. 2. *Hyla crassa*, U.I.M.N.H. No. 25050, Cerro San Felipe, Oaxaca, México. 3. *Plectrohyla laeertosa*, U.I.M.N.H. No. 33693, "Región de Soconusco," Chiapas, México.

### PLATE 5.

1. *Plectrohyla pyenoehila*, T.C.W.C. No. 21459, 5 kilometers north-northwest of san Cristóbal de las Casas, Chiapas, México. 2. *Plectrohyla hartwegi*, U.M.M.Z. No. 94428, Barrejonel, Chiapas, México.

### PLATE 6.

*Hyla miliaria*, K.U. No. 101610 Finca Santa Clara, Chiriquí Province, Panamá; gliding pose, from a field sketch by Linda Trueb.

### PLATE 7.

*Hemipraetetus panamensis*, B.Y.U. No. 19142, Río Changena, Darién Province, Panamá; female carrying young, each attached to dorsum by a pair of double-stranded cords.

### PLATE 8.

Egg clutches: 1. *Hyla pseudopuma pseudopuma* in shallow pond at Tapantí, Cartago Province, Costa Rica. 2. *Hyla lancasteri* on herb above stream on the north slope of Cerro Pando, Bocas del Toro Province, Panamá. 3. *Hyla thorectes* on fern above stream at 37 kilometers north of San Gabriel Mixtepec, Oaxaca, México. 4. *Agalychnis annae*, on branch above pond at La Palma, San José Province, Costa Rica.

### PLATE 9.

1. Nests of *Hyla boans* in creek at the Río Sasardí, Camp Sasardí, San Blas Province, Panamá; note machete for scale. 2. Close-up of nest of *Hyla boans* containing small tadpoles. Both photographs by Charles W. Myers.

### PLATE 10.

1. Pond at Puerto Viejo, Heredia Province, Costa Rica. Ten species of hylids (*Hyla boulengeri*, *elaeoch-*

*roa*, *loquax*, *phlebotodes*, *ebraecata*, *Smilisca baudinii*, *phaeota*, *puma*, *Agalychnis callidryas*, and *A. saltator*) are known to breed in the pond; photographed on June 21, 1966. 2. Pond at 4 kilometers west-northwest of Esparta, Puntarenas Province, Costa Rica. Four species of hylids (*Hyla stauferi stauferi*, *H. microcephala underwoodi*, *Smilisca baudinii*, and *Phrynohyas venulosa*) are known to breed in the pond; photographed on June 22, 1961.

### PLATE 11.

Stream in cloud forest at 3 kilometers southwest of Huatusco, Veracruz, México, elevation 1325 meters. Hylids found along this stream include *Hyla miotympanum*, *mixomaculata*, *nubicola*, and *taeniopus*. *Hyla dendroscarta*, *picta*, *Smilisca baudinii*, *Phrynohyas venulosa*, and *Agalychnis moreletii* occur in the cloud forest.

### PLATE 12.

Mating calls: 1. *Hyla regilla curta*, K.U. Tape No. 271; Todos Santos, Baja California Sur, México; July 9, 1963; 28°C. 2. *Hyla cadaverina*, A.M.N.H. Tape No. 7-6; Sentenac Cañon, San Diego County, California; March 24, 1956; 15.5°C. 3. *Hyla arenicolor*, A.M.N.H. Tape No. 76-1; Chiricahua Mountains, Cochise County, Arizona; June 28, 1958; 23.9°C.

### PLATE 13.

Mating calls of *Hyla eximia*. 1. K.U. Tape No. 596; 8 kilometers northwest of Queretaro, Queretaro, México; June 15, 1966; 21.6°C. 2. A.M.N.H. Tape No. 60-2; 16 kilometers southwest of Huachinango, Puebla, México; August 9, 1956; 17.6°C. 3. A.M.N.H. Tape No. 129-1; 1.6 kilometers east of Buenos Aires, Durango, México; July 3, 1963; 15°C.; second individual in background.

### PLATE 14.

Mating calls: 1. *Hyla euphorbiacea*, K.U. Tape No. 589; 6 kilometers southeast of Oaxaca, Oaxaca, México; August 6, 1966; 21.6°C. 2. *Hyla walkeri*, University of Texas Tape No. 179; 1.6 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, México; June 12, 1958; 19°C. 3. *Hyla plicata*, K.U. Tape No. 597; El Chico Parque Nacional, Hidalgo, México; June 16, 1966; 19°C.

### PLATE 15.

Mating calls: 1. *Hyla miotympanum*, K.U. Tape No. 188; south slope of Volcán San Martín Tuxtla, Veracruz, México; August 11, 1960; 30°C. 2. *Hyla arboreascendens*, K.U. Tape No. 198; 6.5 kilometers south of Campamento Vista Hermosa, Oaxaca, México; June 27, 1962; 19.7°C. 3. *Hyla erythromma*, K.U. Tape 350; 8 kilometers south of Yetla, Oaxaca, México; June 16, 1964; 21.6°C., stream in background.

### PLATE 16.

Mating calls: 1. *Hyla thorectes*, K.U. Tape No. 575; 37 kilometers north of San Gabriel Mixtepec, Oaxaca, México; August 2, 1966; 17.3°C.; stream in background. 2. *Hyla hazelae*, K.U. Tape No. 579; 2 kilometers south of El Punto, Oaxaca, México; August 8, 1966; 18.3°C.; stream in background. 3. *Hyla loquax*, University of Texas Tape No. 283; 1 kilometer east of Río Tonolá, Tabasco, México; June 30, 1959; 25.5°C.; insects in background.



## PLATE 17.

Mating calls: 1. *Hyla godmani*, University of Texas Tape No. 280; 5 kilometers east-southeast of Córdoba, Veracruz, México; June 23, 1959; 28.5°C. 2. *Hyla melanomma melanomma*, K.U. Tape No. 340; 12 kilometers north-northwest of San Gabriel Mixtepec, Oaxaca, México; June 20, 1964; 18.8°C; long note, short note, and section of short note. 3. *Hyla melanomma bivocata*, K.U. Tape No. 160; 6.2 kilometers south of Rayón Mescalapa, Chiapas, México; August 5, 1960; 18.3°C.; long note, short note, and section of short note.

## PLATE 18.

Mating calls: 1. *Hyla bromeliacia*, K.U. Tape No. 162; Finca Chicoyou, near Cobán, Departamento Alta Verapaz, Guatemala; July 17, 1960; 20.7°C. 2. *Hyla sumichrasti*, K.U. Tape No. 581; Portillo Nejapa, 14 kilometers east of El Camarón, Oaxaca, México; August 9, 1966; 20.7°C. 3. *Hyla chaneque*, K.U. Tape No. 356; 4.2 kilometers south of Campamento Vista Hermosa, Oaxaca, México; June 17, 1964; 21.7°C.

## PLATE 19.

Mating calls: 1. *Hyla picta*, Univ. Texas Tape No. 279; Villa Juárez, Puebla, México; June 18, 1959; 19°C. 2. *Hyla smithii*, K.U. Tape No. 343; 17 kilometers north-northwest of San Gabriel Mixtepec, Oaxaca, México; June 20, 1964; 19°C. 3. *Hyla rivularis*, K.U. Tape No. 550; Rama Sur Río Las Vueltas, Heredia Province, Costa Rica; March 29, 1966; 18.4°C.

## PLATE 20.

Mating calls: 1. *Hyla pseudopuma pseudopuma*, K.U. Tape No. 564; Cinchona, Alajuela Province, Costa Rica; April 5, 1966; 17.8°C. 2. *Hyla angustilincata*, K.U. Tape No. 562; Rama Sur Río Las Vueltas, Heredia Province, Panamá; March 31, 1966; 12.8°C. 3. *Hyla boans*, K.U. Tape No. 601; Camp Sasardi San Blas Province, Panamá; January 12, 1967; 26°C.

## PLATE 21.

Mating calls: 1. *Hyla tica*, K.U. Tape No. 547; Tapantí, Cartago Province, Costa Rica; March 26, 1966; 21.0°C. 2. *Hyla debilis*, K.U. Tape No. 559; north slope of Cerro Pando, Bocas del Toro Province, Panamá; May 29, 1966; 18°C. 3. *Hyla uranochroa*, K.U. Tape No. 208; Cinchona, Alajuela Province, Panamá; June 12, 1961; 18.6°C.

## PLATE 22.

Mating calls: 1. *Hyla ruficulus*, K.U. Tape No. 337; 14 kilometers north of San Isidro el General, San José Province, Costa Rica; July 19, 1964; 15.6°C; stream in background. 2. *Hyla salvadorensis*, K.U. Tape No. 569; west slope of Cerro Yuuya, Departamento Francisco Morazán, Honduras; July 5, 1966; 19.3°C. 3. *Hyla legleri*, K.U. Tape No. 210; 15 kilometers southwest of San Isidro el General, San José Province, Costa Rica; April 6, 1961; 23.5°C.

## PLATE 23.

Mating calls: 1. *Hyla pictipes*, K.U. Tape No. 147; Río Poasito, 1 kilometer west of Poasito, Alajuela Province, Costa Rica; June 28, 1961; 15°C. 2. *Hyla colymba*, K.U. Tape No. 290; Laguna, Darién Province, Panamá; July 4, 1963; 24°C. 3. *Hyla rufitela*,

K.U. Tape No. 526; Barro Colorado Island, Canal Zone, Panamá; June 24, 1965; 27°C.; insects in background.

## PLATE 24.

Mating calls: 1. *Hyla lancasteri*, K.U. Tape No. 202; 3 kilometers south of Pavones, Cartago Province, Costa Rica; June 7, 1961; 21.5°C. 2. *Hyla lancasteri*, K.U. Tape No. 513; north slope of Cerro Pando, Bocas del Toro Province, Panamá; May 28, 1966; 16.8°C.; stream in background. 3. *Anotheca spinosa*, K.U. Tape No. 357; 11 kilometers north of Campamento Vista Hermosa, Oaxaca, México; June 28, 1964; 21.5°C.

## PLATE 25.

Mating calls: 1. *Hyla crepitans*, K.U. Tape No. 273; Camp Chagres, Canal Zone, Panamá; June 18, 1963; 25°C.; *Engystomops pustulosus* in background. 2. Possible natural hybrid between *Hyla crepitans* and *Hyla rosenbergi*, A.M.N.H. Tape No. 122; Río Bejuco, Panamá Province, Panamá; June 1, 1962; 26°C. 3. *Hyla rosenbergi*, K.U. No. 529; Río Tuira at Río Mono, Darién Province, Panamá; July 25, 1965; 26.4°C.

## PLATE 26.

Mating calls: 1. *Hyla clacochroa*, K.U. Tape No. 98; Turrialba, Cartago Province, Costa Rica; June 9, 1961; 21°C. 2. *Hyla stauferi stauferi*, K.U. Tape No. 93; San Salvador, Departamento San Salvador, El Salvador; July 10, 1960; 24°C. 3. *Hyla stauferi altae*, K.U. Tape No. 502; 2 kilometers west-southwest of Chepo, Panamá Province, Panamá; June 5, 1966; 25.6°C.

## PLATE 27.

Mating calls: 1. *Hyla rubra*, K.U. Tape No. 612; Santa Cecilia, Napo Province, Ecuador; March 10, 1967; 23.5°C. 2. *Hyla boulengcri*, K.U. Tape No. 511; Summit Cardens, Canal Zone, Panamá; June 8, 1966; 28.5°C. 3. *Hyla rostrata*, K.U. Tape No. 288; 3 kilometers west-southwest of Chepo, Panamá Province, Panamá; June 28, 1963; 27°C.

## PLATE 28.

Mating calls: 1. *Hyla microcephala microcephala*, K.U. Tape No. 19; Palmar Sur, Puntarenas Province, Panamá; April 18, 1961; 28°C. 2. *Hyla phyllobodes*, K.U. Tape No. 6; Puerto Viejo, Heredia Province, Costa Rica; June 16, 1961; 29.3°C.; second individual in background. 3. *Hyla robertmcrtensi*, K.U. Tape No. 41; 32 kilometers north of Arriaga, Chiapas, México; August 4, 1960; 28.5°C.

## PLATE 29.

Mating calls: 1. *Hyla ebraccata*, K.U. Tape No. 129; Moravia de Turrialba, Cartago Province, Costa Rica; July 7, 1961; 19°C. 2. *Hyla subocularis*, K.U. Tape No. 285; Laguna, Darién Province, Panamá; July 6, 1963; 23.4°C. 3. *Hyla sartori*, Univ. Texas Tape No. 293; 6 kilometers east of Tecpán de Galeana, Guerrero, México; July 25, 1959; 26°C.

## PLATE 30.

Mating calls: 1. *Ptychohyla schmidtorum chamulac*, K.U. Tape No. 52; 6.2 kilometers south of Rayón Mescalapa, Chiapas, México; August 5, 1960; 19°C. 2. *Ptychohyla ignicolor*, K.U. Tape 399; 4.2 kilometers south of Rayón Mescalapa, Chiapas, México; June 17, 1964; 20.7°C. 3. Rain call of *Agalychnis callidryas*,

K.U. Tape No. 61; 3 kilometers southeast of La Libertad, Departamento El Petén, Guatemala; July 1, 1960; 30°C.

#### PLATE 31.

Mating calls: 1. *Ptychohylla cuthysanota macrotympaum*, K.U. No. 48; Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, Chiapas, México; June 16, 1960; 18°C. 2. *Ptychohylla leonhardschultzei*, U.M.M.Z. Tape No. 525; Campamento Vista Hermosa, Oaxaca, México; March 30, 1959; 19.5°C. 3. *Ptychohylla spinipollex*, K.U. Tape No. 53; Finca Los Alpes, Departamento Alta Verapaz, Guatemala; July 31, 1961; 22.8°C.; stream in background.

#### PLATE 32.

Mating calls: 1. *Smilisca baudinii*, K.U. Tape No. 74, 1.5 kilometers northwest of Coluteca, Departamento Choluteca, Honduras; July 25, 1961; 19°C. 2. *Smilisca cyanosticta*, K.U. Tape No. 373; 11 kilometers north of Campamento Vista Hermosa, Oaxaca, México; June 28, 1964; 21.3°C. 3. *Smilisca phacota*, K.U. Tape No. 79; 7 kilometers southeast of Piedras Negras, Puntarenas Province, Costa Rica; April 10, 1961; 25°C.

#### PLATE 33.

Mating calls: 1. *Smilisca puma*, K.U. Tape No. 382; 7.5 kilometers west of Puerto Viejo, Heredia Province, Costa Rica; February 19, 1965; 23.5°C. 2. *Smilisca sila*, K.U. Tape No. 385; El Volcán, Chiriquí Province, Panamá; February 5, 1965; 18°C. 3. *Smilisca sordida*, K.U. Tape No. 398; Río Jorco, 2 kilometers south of Desamparados, San José Province, Costa Rica, February 18, 1965; 20.5°C.

#### PLATE 34.

Mating calls: 1. *Pternohyla fodiens*, K.U. Tape No. 584; 16 kilometers north of Mazatlán, Sinaloa, México; August 24, 1967; 26.3°C. 2. *Triprion spatulatus rcticulatus*, L.A.C.M. Tape (specimen L.A.C.M. No. 36815); 12 kilometers southwest of Colima, Colima, México; July 12, 1967; 26.2°C. 3. *Triprion petasatus*, K.U. Tape No. 218; 2.5 kilometers east of Chichén Itzá; Yucatán, México; July 23, 1962; 26.5°C.

#### PLATE 35.

Mating calls: 1. *Acris crepitans*, K.U. Tape No. 331; Rockefeller Experimental Tract, Douglas County, Kansas; May 8, 1964; 15.5°C.; other individuals in background. 2. *Phyllomedusa lemur*, K.U. Tape No. 67; La Palma, San José, Province, Costa Rica; May 8, 1961; 17.7°C.; band of insect noises at about 3500 cycles per second in background. 3. *Plectrohyla ixil*, K.U. Tape No. 543; 6.2 kilometers south of Rayón Mescalapa, Chiapas, México; February 24, 1966; 15°C.; stream in background.

#### PLATE 36.

Mating calls: 1. *Gastrotheca cecratophrys*, K.U. Tape No. 595; Río Claro near junction with Río Changena, Bocas del Toro Province, Panamá; May 23, 1966; 18.5°C.; river in background. 2. *Gastrotheca nicefori*, K.U. Tape 600; South ridge of Cerro Citurio, Serranía de Pirre, Darién Province, Panamá; January 24, 1966; 20°C.; band of insect noises in background. 3. *Phrynohyas venulosa*, K.U. Tape No. 593; Palmar Norte, Puntarenas Province, Costa Rica; April 8, 1966; 24.5°C.

#### PLATE 37.

Mating calls: 1. *Pseudacris clarkii*, A.M.N.H. Tape No. 147; 5 miles north of Independence, Montgomery County, Kansas; June 20, 1965; 21.5°C. 2. *Pachymedusa dacnicolor*, A.M.N.H. Tape No. 27; near Tepic, Nayarit, México; August 16, 1956; 23°C. 3. Release call of *Phyllomedusa venusta*, K.U. Tape No. 527; Río Tuira at Río Mono, Darién Province, Panamá; July 14, 1965; 25.5°C.

#### PLATE 38.

Mating calls: 1. *Agalychnis saltator*, K.U. Tape No. 487; 2 kilometers east of Tilarán, Guanacaste Province, Costa Rica; August 21, 1964; 22.3°C. 2. *Agalychnis callidryas*, K.U. Tape No. 61; 3 kilometers southeast of La Libertad, Departamento El Petén, Guatemala; July 1, 1960; 30°C. 3. *Agalychnis moreletti*, K.U. Tape No. 64; Finca Chicoyou, near Cobán, Departamento Alta Verapaz, Guatemala; August 7, 1961; 21.5°C.; band of insect noises at about 2000 cycles per second in background.

#### PLATE 39.

Mating calls: 1. *Agalychnis annae*, K.U. Tape No. 55; Tapantí, Cartago Province, Costa Rica; April 19, 1961; 20°C. 2. *Agalychnis spurrelli*, K.U. Tape No. 295; Tacarcuna, Darién Province, Panamá, July 16, 1963; 22°C. 3. *Agalychnis litodryas*, K.U. Tape No. 486; Río Tuira at Río Mono, Darién Province, Panamá; July 27, 1965; 16.3°C.

#### PLATE 40.

Release calls: 1. *Pachymedusa dacnicolor*, A.M.N.H. Tape No. 92; 32 kilometers east of Manzanillo, Colima, México; July 22, 1959; 25°C. 2. *Smilisca baudinii*, A.M.N.H. Tape No. 94; 3 kilometers south of the Río Cihuatlán, Colima, México; July 16, 1959; 28.5°C. 3. *Pternohyla fodiens*, A.M.N.H. Tape No. 92; Chapala, Jalisco, México; July 14, 1959.

#### PLATE 41.

1. *Pachymedusa dacnicolor*, U.M.M.Z. No. 115308, 1.6 kilometers northwest of Cuautlixco, Morelos, México. 2. *Phyllomedusa venusta*, K.U. No. 96150, Río Tuira at Río Mono, Darién Province, Panamá.

#### PLATE 42.

1. *Agalychnis saltator*, K.U. No. 86512 (night), 2 kilometers east of Tilarán, Guanacaste Province, Costa Rica. 2. *Agalychnis callidryas*, K.U. No. 96131, Río Tuira at Río Mono, Darién Province, Panamá. 3. *Agalychnis calcarifer*, K.U. No. 77451, Laguna, Darién, Panamá. 4. *Agalychnis saltator*, K.U. No. 86512 (day), 2 kilometers east of Tilarán, Guanacaste Province, Costa Rica. 5. *Agalychnis callidryas*, K.U. No. 63935, 4.2 kilometers west of Puerto Viejo, Heredia Province, Costa Rica.

#### PLATE 43.

1. *Agalychnis morcletii*, K.U. No. 57954, Finca Chicoyou, near Cobán, Departamento Alta Verapaz, Guatemala. 2. *Phyllomedusa lemur*, K.U. No. 63940 (night), Tapantí, Cartago Province, Costa Rica. 3. *Agalychnis annae*, K.U. No. 64020, Tapantí Cartago Province, Costa Rica. 4. *Agalychnis litodryas*, K.U. No. 96149, Río Tuira, at Río Mono, Darién Province, Panamá. 5. *Phyllomedusa lemur*, K.U. No. 63940 (day), Tapantí, Cartago Province, Costa Rica. 6. *Agalychnis spurrelli*, K.U. No. 77499, Barro Colorado Island, Canal Zone, Panamá.



## PLATE 44.

1. *Hyla miliaria*, K.U. No. 101610, Finca Santa Clara, Chiriquí Province, Panamá. 2. *Hemiphractes panamensis*, K.U. No. 107422, south ridge of Cerro Citurio, Serranía de Pirre, Darién Province, Panamá. 3. *Anotheca spinosa*, U.M.M.Z. No. 118173, south slope of Volcán San Martín, Veracruz, México.

## PLATE 45.

1. *Gastrotheca nicefori*, K.U. No. 111991, ridge between Río Jaqué and Río Imamadó, Darién Province, Panamá. 2. *Gastrotheca ceratophrys*, K.U. No. 77016, Laguna, Darién, Panamá.

## PLATE 46.

1-4. *Phrynolias venulosa*, respectively: U.M.N.Z. No. 104814, Barranca Bejuco, Michoacán, México. U.M.M.Z. No. 115237, 5.3 kilometers east-northeast of Encinal, Veracruz, México. U.M.M.Z. No. 119158, 3.5 kilometers south of Villahermosa, Tabasco, México. K.U. No. 64068, 4 kilometers west-northwest of Esparta, Puntarenas Province, Costa Rica.

## PLATE 47.

1. *Hyla staufferi staufferi*, U.M.M.Z. No. 115198, 7 kilometers east-southeast of Córdoba, Veracruz, México. 2. *Hyla staufferi staufferi*, U.M.M.Z. No. 119196, 6.1 kilometers west of Tuxtla Gutiérrez, Chiapas, México. 3. *Hyla staufferi altae*, K.U. No. 116861, 6 kilometers south-southwest of Penonome, Coclé Province, Panamá. 4. *Hyla rubra*, K.U. No. 109472, Santa Cecilia, Napo Province, Ecuador. 5. *Hyla elaeochoa*, K.U. No. 64414, Turrialba, Cartago Province, Costa Rica. 6. *Hyla elaeochoa*, K.U. No. 64499, Laguna Monte Alegre, Alajuela Province, Costa Rica.

## PLATE 48.

1. *Hyla boulengeri*, K.U. No. 64321, 10.5 kilometers west-northwest of Villa Neily, Puntarenas Province, Costa Rica. 2. *Hyla boulengeri*, K.U. No. 95978, 3.2 kilometers west of Almirante, Bocas del Toro Province, Panamá. 3. *Hyla rostrata*, No. 77164, 3 kilometers west of Chepo, Panamá Province, Panamá.

## PLATE 49.

1. *Hyla microcephala microcephala*, K.U. No. 64593, Palmar Sur, Puntarenas Province, Costa Rica. 2. *Hyla microcephala underwoodi*, K.U. No. 64565, Lago de Yojoa, Departamento Cortés, Honduras. 3. *Hyla robertmertensi*, U.M.M.Z. No. 115243, 7 kilometers west-northwest of Tapanatepec, Oaxaca, México. 4. *Hyla phlebodes*, K.U. No. 64798, Turrialba, Cartago Province, Costa Rica. 5. *Hyla sartori*, U.M.M.Z. No. 119225, 12 kilometers west-southwest of Tierra Colorado, Guerrero, México. 6. *Hyla subocularis*, K.U. No. 77348, Laguna, Darién Province, Panamá. 7. *Hyla ebraceata*, K.U. No. 96005, 3.2 kilometers west of Almirante, Bocas del Toro Province, Panamá. 8. *Hyla ebraceata*, K.U. No. 65120, 10.5 kilometers west-northwest of Villa Neilly, Puntarenas Province, Costa Rica.

## PLATE 50.

1. *Hyla rufitela*, K.U. No. 77307, Barro Colorado Island, Canal Zone, Panamá. 2. *Hyla erepitanis*, K.U. No. 80457, Finca La Sumbadora, Panamá Province, Panamá. 3. *Hyla boans*, K.U. 96013, juvenile, Río Tuira at Río Mono, Darién Province, Panamá. 4. *Hyla rosenbergi*, K.U. No. 65015, 10.5 kilometers

west-northwest of Villa Neily, Puntarenas Province, Costa Rica.

## PLATE 51.

1 and 2. *Hyla boans*, K.U. Nos. 108834 and 108835, respectively, Camp Sasardi, San Blas, San Blas Province, Panamá.

## PLATE 52.

1. *Hyla pieadoi*, K.U. No. 64872, Río Poasito, 1 kilometer west of Poasito, Alajuela Province, Costa Rica. 2. *Hyla colymba*, K.U. 95979, Altos de Pacora, Panamá Province, Panamá. 3 and 4. *Hyla angustilicata*, K.U. Nos. 103590 and 103576, respectively, Rama Sur Río las Vueltas, south slope of Volcán Barba, Heredia Province, Costa Rica. 5. *Hyla pseudopuma pseudopuma*, K.U. No. 103715, Cinchona, Alajuela Province, Costa Rica. 6. *Hyla pseudopuma infucata*, K.U. No. 101770, Río Changena, 830 meters, Bocas del Toro Province, Panamá.

## PLATE 53.

1. *Hyla tiea*, K.U. No. 65132, Río María-Aguilar, 3 kilometers west of Cariblanco, Alajuela Province, Costa Rica. 2. *Hyla rivularis*, K.U. No. 64986, La Concordia, Heredia Province, Costa Rica. 3. *Hyla debilis*, K.U. No. 101568, north slope Cerro Pando, 1450 meters, Bocas del Toro Province, Panamá. 4. *Hyla xanthosticta*, K.U. No. 103772, Rama Sur Río las Vueltas, south slope of Volcán Barba, Heredia Province, Costa Rica. 5. *Hyla pictipes*, K.U. No. 64646, ♂, Río Poasito, 1 kilometer west of Poasito, Alajuela Province, Costa Rica. 6. *Hyla pietipes*, K.U. No. 103605, ♀, Rama Sur Río las Vueltas, south slope of Volcán Barba, Heredia Province, Costa Rica.

## PLATE 54.

1. *Hyla rufiochilus*, K.U. No. 65140, 15 kilometers southwest of San Isidro el General, San José Province, Costa Rica. 2. *Hyla lancasteri*, K.U. No. 64729, 3 kilometers south of Pavones, Cartago Province, Costa Rica. 3. *Hyla uranochroa*, K.U. No. 65110, 3 kilometers south of Pavones, Cartago Province, Costa Rica. 4. *Hyla laneasteri*, K.U. No. 101736, north slope of Cerro Pando, 1920 meters, Bocas del Toro Province, Panamá. 5. *Hyla legleri*, K.U. No. 64529, 15 kilometers southwest of San Isidro el General, San José Province, Costa Rica.

## PLATE 55.

1. *Hyla smithii*, U.M.M.Z. No. 115224, 1.6 kilometers south of Temixco, Morelos, México. 2. *Hyla smithii*, K.U. No. 57678, 3 kilometers north of Poichutla, Oaxaca, México. 3. *Hyla godmani*, U.M.M.Z. No. 115171, 7 kilometers east-southeast of Córdoba, Veracruz, México. 4. *Hyla picta*, U.M.M.Z. No. 115260, 7 kilometers east-southeast of Córdoba, Veracruz, México. 5. *Hyla loquax*, K.U. No. 103686, Puerto Viejo, Heredia Province, Costa Rica.

## PLATE 56.

1. *Hyla miotypanum*, U.M.M.Z. No. 118155, ♀, Salto Cola de Caballo, Nuevo León, México. 2-4. *Hyla miotypanum*, U.M.M.Z. No. 115290, 7 kilometers northeast of Huatusco, Veracruz, México, showing metachrosis. 5. *Hyla erythromma*, K.U. No. 87104, 8 kilometers south of Yelita, Oaxaca, México.

## PLATE 57.

1. *Hyla hazelae*, K.U. No. 100968, 2 kilometers south of El Punto, Oaxaca, México. 2. *Hyla thoreetes*,



K.U. No. 100947, 37 kilometers north of San Cabriel Mixtepec, Oaxaca, Mexico. 3. *Hyla arborescandens*, K.U. No. 64316 from Río Octapa, 8 kilometers north-east of Tezuítlan, Puebla, México. 4. *Hyla arborescandens*, K.U. No. 61216 from 4.2 kilometers south of Campamento Vista Hermosa, Oaxaca, México. 5. *Hyla valancifer*, U.M.M.Z. No. 118157, south slope of Volcán San Martín, Veracruz, México.

## PLATE 58.

1. *Hyla melanomma melanomma*, K.U. No. 86954, 12 kilometers north-northeast of San Cabriel Mixtepec, Oaxaca, México. 2. *Hyla melanomma bivocata*, K.U. No. 58446, 6.2 kilometers south of Rayón Mescalapa, Chiapas, México. 3 and 4. *Hyla pinorum*, U.M.M.Z. Nos. 125371 and 125367, respectively, from 1.6 kilometers east of San Andreas della Cruz, Cuerrero, México. 5. *Hyla mixomaculata*, U.M.M.Z. No. 118171, 7.5 kilometers Huatusco, Veracruz, México. 6. *Hyla pcllita*, K.U. No. 100970, 33 kilometers north of San Cabriel Mixtepec, Oaxaca, México. 7. *Hyla pinorum*, K.U. 87612, juvenile, 3.3 kilometers north of San Vicente, Cuerrero, México. 8. *Hyla nubicola*, U.M.M.Z. No. 118160, 3 kilometers southwest of Huatusco, Veracruz, México.

## PLATE 59.

1. *Hyla sumichrasti*, K.U. No. 100935, Portillo Nejapa, 14 kilometers east of El Camarón, Oaxaca, México. 2. *Hyla sumichrasti*, K.U. No. 57851, 2 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, México. 3. *Hyla smaragdina*, K.U. No. 75301, Santa Lucía, Sinaloa, México. 4. *Hyla salvadorensis*, K.U. No. 103256, west slope of Cerro Uyuca, Departamento Francisco-Morazán, Honduras. 5. *Hyla bromclacia*, K.U. No. 57249, Finca Chicoyou, near Cobán, Departamento Alta Verapaz, Guatemala. 6. *Hyla dendroscarta*, U.M.M.Z. No. 118167, Mirador, Veracruz, México.

## PLATE 60.

1. *Hyla altipotens*, K.U. No. 101009, 37 kilometers north of San Cabriel Mixtepec, Oaxaca, México. 2 and 3. *Hyla chaneque*, K.U. Nos. 58439, ♂, and 58442, ♀, respectively, 6.2 kilometers north of Rayón Mescalapa, Chiapas, México.

## PLATE 61.

1 and 2. *Hyla taciopus*, U.M.M.Z. Nos. 118170, ♂, 7.5 kilometers southwest of Huatusco, and 118169, ♀, 3 kilometers southwest of Huatusco, Veracruz, México, respectively. 3. *Hyla altipotens*, K.U. No. 101001, 37 kilometers north of Rayón Mescalapa, Oaxaca, México.

## PLATE 62.

1. *Hyla distincta*, U.M.M.Z. No. 119193, 12.5 kilometers east-northeast of Dos Aguas, Michoacán, México. 2. *Hyla distincta*, A.M.N.H. No. 76422, 1 kilometer northeast of Ayutla, Oaxaca, México. 3 and 4. *Hyla pentheter*, K.U. Nos. 100932, ♂, and 100931, ♀, respectively, 37 kilometers north of San Cabriel Mixtepec, Oaxaca, México.

## PLATE 63.

1. *Hyla charadriicola*, U.M.M.Z. No. 118166, Río Totolapa, 14.4 kilometers west of Huachinango, Puebla, México. 2. *Hyla chryses*, U.M.M.Z. No. 125373, between Puerto Chico and Asolcadero, Cuerrero, México. 3. *Hyla robertsoni*, K.U. No. 57655, El Chico Parque Nacional, Hidalgo, México. 4 and 5. *Hyla siopela*, K.U. Nos. 100990, juvenile, and 100977, ♂, west slope Cofre de Perote, Veracruz, México.

## PLATE 64.

1. *Hyla cadaverina*, K.U. No. 109866, Palm Canyon, Borrego, San Diego County, California. 2. *Hyla arnicolor*, U.M.M.Z. No. 115170, Agua del Obispo, Cuerrero, México. 3. *Hyla arnicolor*, U.M.M.Z. No. 119204 from Chinapa, Michoacán, México. 4. *Pseudacris clarkii*, K.U. No. 110232, 2 miles south of Wau-netka, Jefferson County, Oklahoma. 5. *Acris crepitans*, K.U. No. 116930, Lawrence, Douglas County, Kansas.

## PLATE 65.

1-3. *Hyla regilla hypochondriaca*, K.U. Nos. 109875, 109876, and 109872, respectively, Ramona, San Diego County, California. 4. *Hyla regilla hypochondriaca*, K.U. No. 109871, Borrego, San Diego County, California. 5. *Hyla eximia*, U.N.M. No. 5637, 16 miles south of Springerville, Apache County, Arizona.

## PLATE 66.

1 and 3. *Hyla eximia*, K.U. Nos. 86993 and 86991, respectively, 3.5 kilometers west of Cuautlixco, Morelos, México. 2. *Hyla plicata*, K.U. No. 57389, El Chico Parque Nacional, Hidalgo, México. 4 and 5. *Hyla walkeri*, K.U. Nos. 57832 and 57836, 18 kilometers northwest of Comitán, Chiapas, México. 6. *Hyla euphorbiacca*, K.U. No. 57346, 8 kilometers southeast of Oaxaca, Oaxaca, México.

## PLATE 67.

1. *Ptychohyla schmidtorum schmidtorum*, K.U. No. 58035, Finca La Paz, near La Reforma, Departamento San Marcos, Guatemala. 2. *Ptychohyla schmidtorum chamulac*, K.U. No. 58069, 6.2 kilometers south of Rayón Mescalapa, Chiapas, México. 3. *Ptychohyla ignicolor*, U.M.M.Z. 119062, Campamento Vista Hermosa, Oaxaca, México. 4. *Ptychohyla euthysanota euthysanota*, K.U. No. 58001, Finca La Paz, near La Reforma, Departamento San Marcos, Guatemala. 5. *Ptychohyla euthysanota macrotympanum*, K.U. No. 58047, Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, Chiapas, México. 6. *Ptychohyla leonhardschultzei*, U.M.M.Z. 115514, 8 kilometers south of Yetla, Oaxaca, México. 7. *Ptychohyla spinipollex*, K.U. No. 58054, Finca Los Alpes, Departamento Alta Verapaz, Guatemala.

## PLATE 68.

1. *Plectrohyla matudai*, K.U. No. 58869, Finca La Paz, near La Reforma, Departamento San Marcos, Guatemala. 2. *Plectrohyla ixil*, K.U. No. 58853, 5.6 kilometers south of Rayón Mescalapa, Chiapas, México. 3. *Plectrohyla sagorum*, K.U. No. 103164, Granja Lorena, 13 kilometers north-northeast of Colomba, Departamento Quetzaltenango, Guatemala. 4. *Plectrohyla quecchi*, K.U. 64107, Finca Los Alpes, Departamento Alta Verapaz, Guatemala.

## PLATE 69.

1 and 2. *Plectrohyla glandulosa*, K.U. 58703, ♂, and 58715, ♀, respectively, 8 kilometers south of Paquix, Departamento Huehuetenango, Guatemala. 3. *Plectrohyla guatemalensis*, K.U. No. 58831, Finca Los Alpes, Departamento Alta Verapaz, Guatemala. 4. *Plectrohyla avia*, K.U. 94016, Volcán Tacaná, 8 kilometers north of Unión Juárez, Chiapas, México.

## PLATE 70.

1. *Smilisca phacota*, K.U. No. 64291, Quebrada Boruca, 22 kilometers east of Palmar Norte, Puntarenas Province, Costa Rica. 2. *Smilisca phacota*, K.U.

No. 64281, Moravia, Cartago Province, Costa Rica. 3. *Smilisca cyanosticta*, U.M.M.Z. No. 118163, south slope of Volcán San Martín, Veracruz, México. 4. *Smilisca baudinii*, K.U. No. 64159, 4 kilometers west-northwest of Esparta, Puntarenas Province, Costa Rica. 5. *Smilisca baudinii*, U.M.M.Z. No. 115179, 2 kilometers west of Xicotencatl, Tamaulipas, México.

PLATE 71.

1. *Smilisca sordida*, K.U. No. 91757, Río Jorco, 2 kilometers south of Desamparados, San José Province, Costa Rica. 2. *Smilisca sordida*, K.U. No. 64257, 20 kilometers southwest of San Isidro el General, San José Province, Costa Rica. 3. *Smilisca sila*, K.U. No. 80481, Finca La Sumbadora, Panamá Province, Panamá. 4. *Smilisca sila*, Finca Palosanto, 6 kilome-

ters west-northwest of El Volcán, Chiriquí Province, Panamá. 5. *Smilisca puma*, K.U. No. 103811, Puerto Viejo, Heredia Province, Costa Rica.

PLATE 72.

1. *Triprrion petasatus*, K.U. No. 71448, 7.5 kilometers west of Escárcega, Campeche, México. 2. *Triprrion spatulatus reticulatus*, U.M.M.Z. No. 115321, 8.6 kilometers west of Tehuantepec, Oaxaca, México. 3. *Triprrion spatulatus spatulatus*, U.M.M.Z. No. 115322, 30 kilometers north-northwest of Mazatlán, Sinaloa, México. 4. *Pternohyla fodiens*, U.M.M.Z. 115298, 31.3 kilometers north-northwest of Mazatlán, Sinaloa, México. 5. *Pternohyla fodiens*, U.M.M.Z. 115299, juvenile, 5.6 kilometers north-northwest of Mazatlán, Sinaloa, México.

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# INDEX

- abbreviations for collections, 7  
*Acris*, 19, 20, 645-647  
*Acrodytes*, 161  
*adipoventris*, *Ptychohyla*, 518, 541  
*affinis*, *Hyla*, 514  
*Agalychnis*, 18, 87-98  
*albomarginata*, *Hyla*, 173, 240  
*alcorni*, *Agalychnis*, 83  
     *Phyllomedusa*, 83  
*alleci*, *Hyla*, 302  
*Allophryne*, 19, 20  
*altae*, *Hyla*, 199  
     *Hyla staufferi*, 199-200, 713, 731, 733, pls. 26, 47  
*altipotens*, *Hyla*, 450-453, 697, 734, pls. 60, 61  
*alvaradoi*, *Hyla*, 328  
*Amphignathodon*, 18, 20  
*Amphignathodontidae*, 18  
*Amphignathodontinae*, 18  
*Amphodus*, 19, 173  
*angustilineata*, *Hyla*, 273-276, 697, 731, 733, pls. 20, 52  
*annae*, *Agalychnis*, 117-120, 695, 730, 732, pls. 8, 39, 43  
     *Phyllomedusa*, 117  
*Anotheca*, 18, 20, 144-145  
*Aparasphenodon*, 19, 20  
*Aplastodiscus*, 19, 20  
*arborea*, *Rana*, 173  
*arborescandens*, *Hyla*, 380-384, 697, 730, 734, pls. 15, 57  
*arboricola*, *Hyla*, 499, 694  
*arenicolor*, *Hyla*, 493, 514-518, 697, 730, 734, pls. 12, 64  
*Argenteohyla*, 19, 20  
*Auletris*, 173  
*aurata*, *Hyla*, 173  
*aurea*, *Hyla*, 173  
*avia*, *Plectrohyla*, 578-580, 720, 734, pl. 69  
*axillamembrana*, *Hyla*, 359  
*azteca*, *Hyla*, 413  
     *Hyllella*, 413  
*baudinii*, *Hyla*, 585, 594  
     *Hyla baudinii*, 594  
     *Smilisca*, 594-598, 723, 732, 735, pls. 32, 40, 70  
     *Smilisca baudinii*, 594  
*beltrani*, *Hyla*, 594  
*bicolor*, *Phyllomedusa*, 130  
     *Rana*, 130  
     *biseriata*, *Hyla euphorbiacea*, 510  
*bistincta*, *Hyla*, 457-462, 698, 734, pl. 62  
     *Hyla bistincta*, 457  
*bivocata*, *Hyla*, 402  
     *Hyla melanomma*, 402-403, 705, 731, 734, pls. 17, 58  
*Boana*, 173  
*boans*, *Hyla*, 258-261, 699, 730, 731, 733, pls. 9, 20, 50, 51  
     *Rana*, 173, 258  
*bocourti*, *Hyla*, 505  
     *Hylola*, 505, 694  
*bogertae*, *Hyla*, 479-482, 699  
*bogerti*, *Ptychohyla*, 535  
*bogotensis*, *Hylonomus*, 173  
*boulengeri*, *Hyla*, 200-204, 312, 699, 731, 733, pls. 27, 48  
     *Scyttopis*, 200  
*brachycephala*, *Plectrohyla*, 559  
     *Plectrohyla matudai*, 559  
*Bradymedusa*, 130  
 breeding cycles, 656  
     sites, 655  
     time of, 654  
*bromeliacia*, *Hyla*, 429-434, 699, 731, 734, pls. 18, 59  
*bromeliana*, *Hyla*, 445  
*bufonia*, *Hyla*, 163  
*cadaverina*, *Hyla*, 493-496, 699, 730, 734, pls. 12, 64  
*caerulea*, *Rana*, 173  
*Calamita*, 173  
*calcarifer*, *Agalychnis*, 120-124, 695  
     *Phyllomedusa*, 120  
*californiae*, *Hyla*, 493  
*callidryas*, *Agalychnis*, 102-112, 695, 731, 732, pls. 30, 38, 42  
     *Hyla*, 102  
     *Phyllomedusa*, 102  
     *callidryas*, *Phyllomedusa*, 102  
     *taylori*, *Phyllomedusa*, 102  
*cardenasi*, *Hyla*, 499, 694  
*Cauphias*, 547  
*Centrotelma*, 173  
*Cephalophractus*, 161  
*Cerathyla*, 19, 138, 694  
*ceratophrys*, *Gastrotheca*, 153-158, 697, 732, 733, pls. 36, 45  
     *Hyla*, 153  
*chamulae*, *Ptychohyla*, 531  
     *Ptychohyla schmidtorum*, 531-532, 723, 731, 734, pls. 30, 67  
*chaneque*, *Hyla*, 440-445, 694, 699, 731, 734, pls. 18, 60  
 character states, 660-667  
*charadricola*, *Hyla*, 466-468, 699, 734, pl. 63  
*cherrei*, *Hyla*, 650  
*chica*, *Hyla*, 10  
*Chirodryas*, 173  
*Chlorophilus*, 641  
 chromosomes, number of, 54  
*chryses*, *Hyla*, 468-470, 700, 734, pl. 63  
*Cinclidium*, 173  
*Cincloscopus*, 173  
*clarkii*, *Chlorophilus triseriatus*, 642  
     *Helocaetes*, 642  
     *Pseudacris*, 642-645, 721, 732, 734, pls. 37, 64  
     *Pseudacris triseriata*, 642  
 clutch size, 657  
*colymba*, *Hyla*, 328-332, 700, 731, 733, pls. 23, 52  
 continental drift, 677  
*coper*, *Hyla*, 514  
*Cophomantis*, 173  
*copii*, *Hyla*, 514

- corasterias*, *Plurynohyas*, 163  
*coronata*, *Anothea*, 145  
     *Gastrotheca*, 145  
*Corythomantis*, 19, 20  
*cotzieensis*, *Plectrohyla*, 572  
*craspedopus*, *Agalychnis*, 89  
*crassa*, *Hyla*, 477-479, 700, 730, pl. 4  
*crassum*, *Cauphias*, 477  
*crassus*, *Cauphias*, 477  
     *Hypsiboas*, 477  
*crepitans*, *Aeris*, 647-649, 695, 732, 734, pls. 35, 64  
     *Hyla*, 173, 247-253, 694, 700, 731, 733, pls. 25, 50  
     *Hypsiboas*, 247  
*Cryptobatrachus*, 18, 20  
*eulex*, *Hyla*, 196  
*curta*, *Hyla*, 490  
     *Hyla regilla*, 490-491, 710, 730, pls. 1, 12  
*cyanosticta*, *Hyla phacota*, 598  
     *Smilisca*, 598-603, 727, 732, 735, pls. 32, 70  
     *Smilisca phacota*, 598  
*cyclomaculata*, *Hyla*, 445  
  
*daenicolor*, *Agalychnis*, 81  
     *Pachymedusa*, 81-87, 717, 732, pls. 37, 40, 41  
     *Phyllomedusa*, 81  
*dalquesti*, *Hyla*, 445  
*darlingi*, *Hyla*, 372, 694  
*dasynota*, *Hyla*, 173  
*daudiinii*, *Smilisca*, 594  
*daulimia*, *Smilisca*, 585, 594  
*debilis*, *Hyla*, 289-292, 700, 731, 733, pls. 21, 53  
*Dendrohyas*, 173  
*Dendropsophus*, 173  
*dendroseata*, *Hyla*, 434-437, 700, 734, pl. 59  
*dentata*, *Pternohyla*, 621-624, 721, 730, pl. 2  
*deserticola*, *Hyla regilla*, 491-694  
*Diaglena*, 19, 628  
*digueti*, *Hyliola*, 514  
distribution, altitudinal, 668  
     ecological, 663  
     geographical, 671  
divergence index, 662  
*dolomedes*, *Hyla baudinii*, 603  
*Dryophytes*, 173  
*duellmani*, *Hyla*, 440, 694  
*dulensis*, *Hyla*, 188  
  
*ebriacea*, *Hyla*, 227-234, 700, 731, 733, pls. 29, 49  
*echinata*, *Hyla*, 346-348, 701, 730, pl. 2  
ecology, moisture requirements, 663  
     tadpoles, 658  
     temperature, 665  
*elacochroa*, *Hyla*, 183, 188-193, 701, 731, 733, pls. 26, 47  
*elegans*, *Fanechonia*, 173  
*Epedaphus*, 173  
*erythromma*, *Hyla*, 392-395, 701, 730, 733, pls. 15, 56  
*euphorbiacea*, *Hyla*, 505-510, 694, 701, 730, 734, pls. 14, 66  
*euthysanota*, *Hyla*, 535, 544  
     *Ptychohyla*, 535  
     *Ptychohyla euthysanota*, 535-539, 722, 734, pl. 67  
evolution, Mesoamerican hylids, 678  
     Nearctic hylids, 691  
     Neotropical hylids, 686  
*Exerodonta*, 173  
*eximia*, *Hyla*, 196, 368, 499-504, 694, 702, 730, 734, pls. 13, 65, 66  
     *Hyla eximia*, 499  
  
*Fanechonia*, 173  
*finbrimembra*, *Hyla*, 348-350, 694, 704, 730, pl. 3  
*Flectonotus*, 18, 20  
*fodiens*, *Pternohyla*, 618, 624-628, 721, 732, 735, pls. 34, 40, 72  
*foliamorta*, *Hyla*, 204  
*forbesi*, *Hyla*, 380  
*freycineti*, *Hyla*, 173  
*Fritziana*, 18, 20  
*frontalis*, *Hyla*, 173  
  
*gabbi*, *Hyla*, 613  
     *Smilisca*, 614  
*galeatus*, *Cephalophractus*, 161  
*Gastrotheca*, 18, 20, 151-153, 651  
*gladulosa*, *Hyla*, 572  
     *Plectrohyla*, 572-575, 720, 734, pl. 69  
*godmani*, *Hyla*, 356-359, 372, 541, 704, 731, 733, pls. 17, 55  
*gracilipes*, *Hyla*, 496, 499  
     *grauulatum*, *cinclidium*, 173  
*gratiosa*, *Hyla*, 173  
*gryllus*, *Aeris*, 642  
*guatemalensis*, *Cauphias*, 580  
     *Hyla*, 580  
     *Plectrohyla*, 580-583, 720, 734, pl. 69  
*Guntheria*, 173  
  
habitats, definition of, 666  
*Habrahyla*, 19  
*hartwegi*, *Plectrohyla*, 583-585, 721, 730, pl. 5  
*hazela*, *Hyla*, 385-388, 704, 730, 733, pls. 16, 57  
*hebes*, *Seytopis*, 161  
*helenae*, *Agalychnis*, 102  
     *Phyllomedusa*, 102  
*Helocactes*, 641  
*Hemiphractinae*, 18  
*Hemiphractus*, 18, 20, 138-140, 694  
*holochroa*, *Hyla*, 112  
*Hyas*, 173  
*Hyla*, 19, 20, 173-176  
     sp., 651-653  
     *albomarginata* group, 239-240  
     *bistincta* group, 453-457  
     *boas* group, 245-247  
     *bogotensis* group, 327-328  
     *bromeliacea* group, 429  
     *erythromma* group, 391-392  
     *eximia* group, 482-484  
     *godmani* group, 355  
     *hazela* group, 384-385  
     *lancasteri* group, 311-312  
     *leucophyllata* group, 226-227  
     *microcephala* group, 207-210  
     *miliaria* group, 341  
     *miotympanum* group, 370-372  
     *mixomaculata* group, 416  
     *parviceps* group, 234-235

- picta* group, 363-365  
*pictipes* group, 294-295  
*pinorum* group, 395-397  
*pseudopuma* group, 261-262  
*rivularis* group, 276-278  
*rubra* group, 176-183  
*salvadorensis* group, 332-333  
*sumichrasti* group, 408-409  
*taeniopus* group, 437-439  
*uranochroa* group, 301-302  
*versicolor* group, 513-514  
*zeteki* group, 318-319  
*Hylaplesia*, 173  
*Hylaria*, 173  
*Hylella*, 173  
Hylidae, 18  
hylid faunas, 678  
Hylina, 19  
Hylinae, 19  
*Hyllola*, 173  
*Hylomantis*, 130  
*Hylomedusa*, 173  
*Hylonomus*, 173  
*Hyloscirtus*, 19, 173  
*hypochondriaca*, *Hyla regilla*, 491-493, 694, 710, 734, pl. 65  
*Hyla scapularis* var., 491  
*Hypsiboas*, 173  
*Hypsiposopus*, 173  
*ignicolor*, *Ptychohyla*, 532-534, 722, 731, 734, pls. 30, 67  
*immensa*, *Hyla*, 352, 694  
*inflata*, *Acrodytes*, 163  
*Phrynohyas*, 163  
*infucata*, *Hyla pseudopuma*, 271-272, 710, 733, pl. 52  
*infulata*, *Hyla*, 173  
*ixil*, *Plectrohyla*, 563-566, 721, 732, 734, pls. 35, 68  
*jacksoni*, *Hyla*, 173  
*labeculata*, *Hyla bistincta*, 457  
*lacetosa*, *Plectrohyla*, 577-578, 721, 730, pl. 4  
*lafrentzi*, *Hyla*, 496  
*Hyla regilla*, 496  
*lancasteri*, *Hyla*, 312-318, 704, 730, 731, 733, pls. 8, 24, 54  
*laticeps*, *Hyla regilla*, 490  
*latifasciata*, *Phrynohyas*, 163  
*legleri*, *Hyla*, 333-337, 704, 731, 733, pls. 22, 54  
*lemur*, *Agalychnis*, 132  
*Phyllomedusa*, 132-135, 720, 732, pls. 35, 43  
*leonhardschultzei*, *Hyla*, 518, 541  
*Ptychohyla*, 403, 541-544, 722, 732, 734, pls. 31, 67  
*Leptopelis*, 19  
*leucophyllata*, *Hyla*, 227  
*lichenosa*, *Hyla*, 163  
*Limnaoedus*, 19, 20, 173  
*litodryas*, *Agalychnis*, 128-130, 696, 732, pls. 39, 43  
*Phyllomedusa*, 128  
*Litoria*, 173  
*Lobipes*, 173  
*Lophopus*, 173  
*loquax*, *Hyla*, 359-363, 705, 730, 733, pls. 16, 55  
*lythrodes*, *Hyla*, 307, 694  
*macrotympanum*, *Hyla*, 539  
*Ptychohyla*, 539  
*Ptychohyla euthysanota*, 539-540, 722, 732, pls. 31, 67  
*manisorum*, *Hyla*, 594  
*marmorata*, *Hyla*, 173  
*Hyla molitor* Variet., 650  
*marmoratus*, *Trachycephalus*, 173  
*marsupiata*, *Hyla*, 151  
*marsupiatum*, *Nototrema*, 145  
*martini*, *Hyla microcephala*, 215  
mating calls, characteristics, 64  
*matudai*, *Plectrohyla*, 559-563, 721, 734, pl. 68  
*Plectrohyla matudai*, 559  
*maxima*, *Calamita*, 258  
*Hyla*, 258  
*Rana*, 258  
measurements, 21  
*melanomma*, *Hyla*, 397-398  
*Hyla melanomma*, 398-402, 705, 731, 734, pls. 17, 58  
*microcephala*, *Hyla*, 210-211, 215  
*Hyla microcephala*, 211-215, 650, 705, 731, 733, pls. 28, 49  
*microcephala* x *underwoodi*, *Hyla microcephala*, 706  
*microeximia*, *Hyla*, 499  
*microtis*, *Hyla*, 372  
*miliaria*, *Hyla*, 352-355, 694, 707, 730, 733, pls. 6, 44  
*Plectrohyla*, 352  
*miliarius*, *Hypsiboas*, 352  
*milleri*, *Hyla*, 541  
*miotympanum*, *Hyla*, 356, 372-380, 694, 707, 730, 733, pls. 15, 56  
*mixe*, *Hyla*, 425-427, 708, 730, pl. 1  
*mixomaculata*, *Hyla*, 416-421, 708, 734, pl. 58  
*mocquardi*, *Hyla*, 10  
*modesta*, *Acrodytes*, 163  
*Phrynohyas*, 163  
*moesta*, *Hyla*, 295  
*Hyla punctariola*, 295  
*molitor*, *Hyla*, 650-651  
*monticola*, *Hyla*, 295  
*Hyla punctariola*, 295  
*moraviaensis*, *Hyla*, 312  
*moreletii*, *Agalychnis*, 112-116, 696, 732, pls. 38, 43  
*Hyla*, 112  
*Phyllomedusa*, 112  
morphological characters, analysis of, 660  
*muricolor*, *Hyla*, 594  
*nana*, *Hyla*, 368  
*nebulosa*, *Hyla*, 493  
*nicefori*, *Gastrotheca*, 158-160, 697, 732, 733, pls. 36, 45  
*nigripes*, *Hyla*, 614  
*nigrita*, *Rana*, 641  
*nigrogrisea*, *Pseudohyla*, 173  
*nigromaculatus*, *Trachycephalus*, 161  
*nigropunctata*, *Hyla*, 163  
*nomina dubita*, 649-650  
*Notodelphys*, 151



- Nototheca*, 19  
*Nototrema*, 151  
*nubicola*, *Hyla*, 423-425, 708, 734, pl. 58  
*Nyctimantis*, 18, 19, 20  
*Nyctimystes*, 19, 20  
  
*oaxacae*, *Hyla bivocata*, 398  
*ocularis*, *Hylodes*, 173  
*Ololygon*, 173  
*Opisthodelphys*, 151  
*Osteocephalus*, 19, 20  
*Osteopilus*, 173  
*ovifera*, *Notodclphys*, 151  
*Opisthodelphys*, 145  
*oviposition sites*, 657  
  
*pachyderma*, *Hyla*, 473-475, 708, 730, pl. 4  
*Pachymedusa*, 18, 19, 81  
*paenulata*, *Hyla*, 163  
*Palmatorappia*, 173  
*palmata*, *Hyla*, 173  
*panamensis*, *Cerathyla*, 140  
*Hemiphractus*, 140-144, 697, 730, 733, pls. 7, 44  
*pansosana*, *Hyla*, 594  
*pellita*, *Hyla*, 421-423, 708, 734, pl. 58  
*Pelobius*, 173  
*Pelodryas*, 173  
*peutheter*, *Hyla*, 462-466, 708, 734, pl. 62  
*petasatus*, *Pharyngodon*, 628, 637  
*Triprion*, 637-641, 729, 732, pls. 34, 72  
*phaeota*, *Hyla*, 598, 603  
*Hyla phaeota*, 603  
*Smilisca*, 603-607, 727, 732, pls. 32, 70  
*phantasmagoria*, *Hyla*, 352, 694  
*Pharyngodon*, 628  
*phlebobdcs*, *Hyla*, 215, 220-223, 708, 731, 733, pls. 28, 49  
*Phrynohyas*, 19, 20, 160-163  
*Phrynomedusa*, 130  
*Phyllobius*, 173  
*Phyllodytes*, 19, 20  
*Phyllomedusa*, 18, 130-132  
*Phyllomedusinae*, 18  
*Phyllomedusidae*, 18  
*picadoi*, *Hyla*, 319-323, 708, 733, pl. 52  
*picta*, *Hyla*, 365-367, 708, 731, 733, pls. 19, 55  
*Hylella*, 365  
*pictipes*, *Hyla*, 295-300, 709, 731, 733, pls. 23, 53  
*Hyla punctariola*, 295  
*pinorum*, *Hyla*, 403-408, 709, 734, pl. 58  
*Pithecopus*, 130  
*platycephala*, *Hylclla*, 409  
*Plectrohyla*, 19, 20, 547-559  
*plicata*, *Hyla*, 496-499, 709, 730, 734, pls. 14, 66  
*preparation of specimens*, 6  
*prevomerine teeth*, number of, 51  
*proboscidea*, *Hyla*, 445  
*Pseudacris*, 19, 20, 641-642  
*Pseudohyla*, 173  
*pseudopuma*, *Hyla*, 262-263  
*Hyla pseudopuma*, 263-271, 710, 730, 731, 733, pls. 8, 20, 52  
*Pternohyla*, 19, 20, 618-621  
*Ptychohyla*, 19, 20, 518-527  
  
*pugnax*, *Hyla*, 247, 694  
*puma*, *Hyla*, 607  
*Smilisca*, 607-609, 728, 732, 735, pls. 33, 71  
*punctariola*, *Hyla*, 10, 295  
*punctata*, *Hyla*, 173  
*punctillata*, *Cophomantis*, 173  
*pynochila*, *Plectrohyla*, 575-577, 721, 730, pl. 5  
  
*quecchi*, *Plectrohyla*, 569-571, 721, 734, pl. 68  
*quinquevittata*, *Hyla*, 188  
  
*raniformis*, *Chirodrysas*, 173  
*Ranoidea*, 173  
*regilla*, *Hyla*, 173, 484-489  
*Hyliola*, 490  
*resinifictrix*, *Hyla*, 163  
*reticulata*, *Diaglena*, 636  
*Diaglena spatulata*, 636  
*reticulatus*, *Triprion spatulatus*, 636-637, 729, 732, 735, pls. 34, 72  
*richardi*, *Hyla*, 348  
*richardtaylori*, *Hyla*, 348, 694  
*rickardsi*, *Hyla*, 356  
*riularis*, *Hyla*, 284-289, 710, 731, 733, pls. 19, 53  
*robertmertensi*, *Hyla*, 217-220, 710, 731, 733, pls. 28, 49  
*robertsorum*, *Hyla*, 470-473, 711, 734, pl. 63  
*robustofemora*, *Hyla*, 477  
*rosenbergi*, *Hyla*, 253-258, 711, 731, 733, pls. 25, 50  
*rostrata*, *Hyla*, 204-207, 711, 731, 733, pls. 27, 48  
*rozellae*, *Hyla*, 535  
*Ptychohyla*, 535  
*ruber*, *Scytotis*, 183  
*Auletris*, 183  
*Calamita*, 183  
*Dendrohyas*, 183  
*Hyla*, 183-188, 711, 731, 733, pls. 27, 47  
*rudis*, *Hyla*, 624  
*rufioculis*, *Hyla*, 307-311, 694, 711, 731, 733, pls. 22, 54  
*rufitela*, *Hyla*, 240-245, 711, 731, 733, pls. 23, 50  
*ruthveni*, *Allophryne*, 20  
  
*sagorum*, *Plectrohyla*, 566-569, 721, 734, pl. 68  
*saltator*, *Agalychnis*, 99-102, 696, 732, pls. 38, 42  
*Phyllomedusa*, 99  
*salvadorensis*, *Hyla*, 337-341, 712, 731, 734, pls. 22, 59  
*salvini*, *Hyla*, 614  
*sartori*, *Hyla*, 223-226, 712, 731, 733, pls. 29, 49  
*Hyla microcephala*, 223  
*schmidtorum*, *Ptychohyla*, 527  
*Ptychohyla schmidtorum*, 527-531, 723, 734, pl. 67  
*Sciux*, 173  
*Scytotis*, 161  
*seasonal activity*, 665  
*senicula*, *Hyla*, 173  
*septentrionalis*, *Hyla*, 173  
*shrevei*, *Hyla*, 10  
*sila*, *Smilisca*, 609-613, 728, 732, 735, pls. 33, 71  
*siopela*, *Hyla*, 475-477, 712, 734, pl. 63  
*smaragdina*, *Hyla*, 413-416, 712, 734, pl. 59  
*Smilisca*, 19, 20, 585-594  
*smithii*, *Hyla*, 368-370, 712, 731, 733, pls. 19, 55

- sordida*, *Hyla*, 613  
*Smilisca*, 613-618, 728, 732, 735, pls. 33, 71  
*spatulata*, *Diaglena*, 634  
*Diaglena spatulata*, 634  
*spatulatus*, *Tripriion*, 628, 629-632  
*Tripriion spatulatus*, 632-636, 729, 735, pl. 72  
 species inquierienda, 651, 717  
*Sphaenorhynchus*, 19, 20  
*spilomma*, *Aerodytes*, 163  
*Hyla*, 163  
*Plirynohyas*, 163  
*spinipollex*, *Hyla*, 544  
*Ptychohyla*, 337, 544-547, 723, 731, 734, pls. 31, 67  
*spinosa*, *Anothea*, 145-151, 697, 731, 733, pls. 24, 44  
*Hyla*, 145  
*splendens*, *Hyla*, 651  
*spurrelli*, *Agalychnis*, 124-128, 697, 732, pls. 39, 43  
*Phyllomedusa*, 124  
*stadelmani*, *Hyla*, 359  
*staufferi*, *Hyla*, 193-195  
*Hyla eximia*, 196  
*Hyla staufferi*, 195-199, 714, 731, 733, pls. 26, 47  
*Stefania*, 19, 20  
*strigilata*, *Hyla*, 173  
*subocularis*, *Hyla*, 235-239, 716, 731, 733, pls. 29, 49  
*sumichrasti*, *Exerodonta*, 409  
*Hyla*, 409-413, 716, 731, 734, pls. 18, 59  
*Hylella*, 409  
 synonymies, 6  
 synonymy, alphabetical, 12  
 tadpoles, developmental time, 659  
     diagnostic features, 38  
     ecology, 658  
*taeniopus*, *Hyla*, 445-450, 716, 734, pl. 61  
*tenera*, *Hylella*, 173  
*Tetrapriion*, 19  
*thorectes*, *Hyla*, 388-391, 716, 730, 733, pls. 8, 16, 57  
*thysanota*, *Hyla*, 350-352, 716, 730, pl. 3  
*tibiatrix*, *Hyla*, 161  
*Hyla tibiatrix*, 163  
*tica*, *Hyla*, 278-284, 716, 731, 733, pls. 21, 53  
*Trachycephalus*, 19, 20, 161  
*Tripriion*, 19, 20, 628-629  
*Tripriioninae*, 20  
*triseriata*, *Hyla*, 641  
*underwoodi*, *Hyla*, 215, 223  
*Hyla microcephala*, 215-217, 706  
*uranochoa*, *Hyla*, 302-306, 716, 731, 733, pls. 21, 54  
*valancifer*, *Hyla*, 342-346, 717, 730, 734, pls. 2, 57  
*vauvletii*, *Hyla*, 594  
*venulosa*, *Aerodytes*, 163  
*Hyla*, 161, 163  
*Hyla venulosa*, 163  
*Plirynohyas*, 163-172, 718, 732, 733, pls. 36, 46  
*Rana*, 160, 163  
*Seytopis*, 163  
*venusta*, *Phyllomedusa*, 135-138, 720, 732, pls. 37, 41  
*vermiculata*, *Hyla*, 163  
*versicolor*, *Hyla*, 173  
*viridis*, *Hyla*, 173  
*vociferans*, *Hyla*, 594  
*walkeri*, *Hyla*, 510-513, 717, 730, 734, pls. 14, 66  
*wellmanorum*, *Hyla*, 607  
*Smilisca*, 607  
 West Indian hylids, 692  
*weyerae*, *Hyla*, 227  
*wrightorum*, *Hyla*, 499  
*Hyla eximia*, 499  
*Hyla regilla*, 499, 694  
*xanthostieta*, *Hyla*, 292-294, 717, 733, pl. 53  
*xerophilla*, *Hyla*, 173, 247  
*zeteki*, *Hyla*, 323-327, 717, 730, pl. 1  
*zonata*, *Hyla*, 160, 163  
*Plirynohyas*, 161, 163





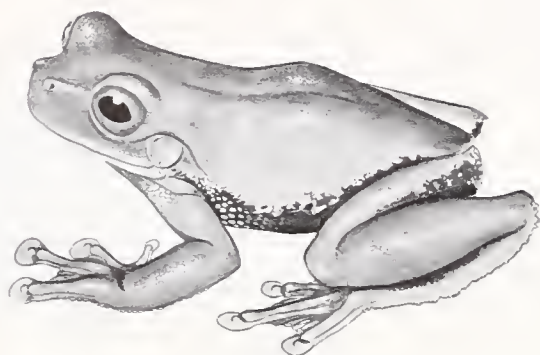






1. *Hyla zeteki*. 2. *Hyla mixe*. 3. *Hyla regilla curta*.  $\times 2$ .

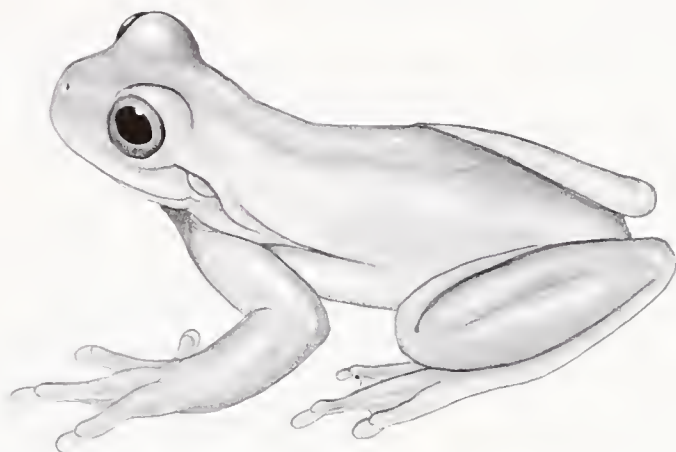




1. *Pterohyla dentata*. 2. *Hyla echinata*. 3. *Hyla valancifer*.  $\times 1$ .

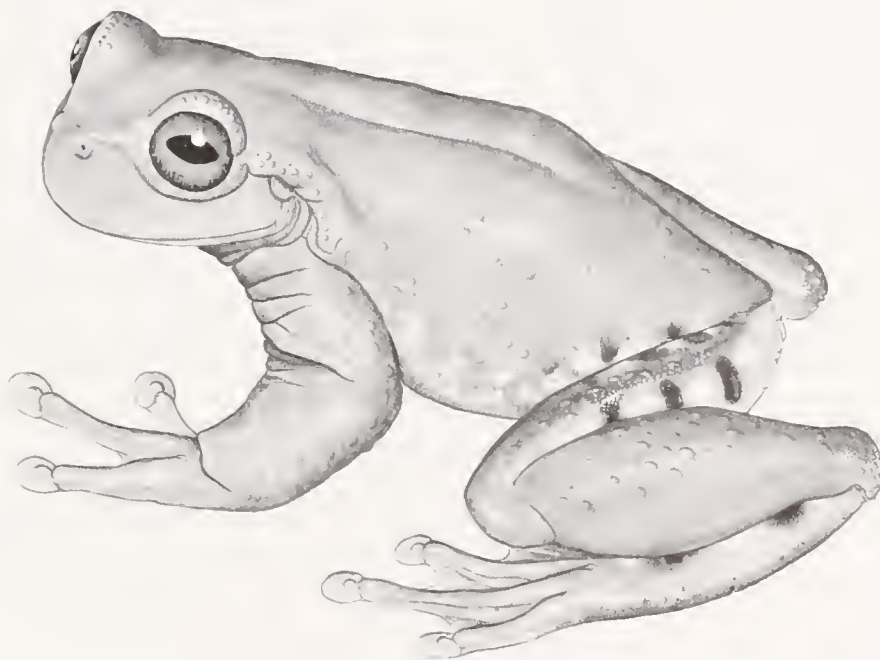


1. *Hyla fimbriembra*. 2. *Hyla thysanota*.  $\times 1$ .



1. *Hyla pachyderma*. 2. *Hyla crassa*. 3. *Plectrohyla lacertosa*.  $\times 1.5$ .

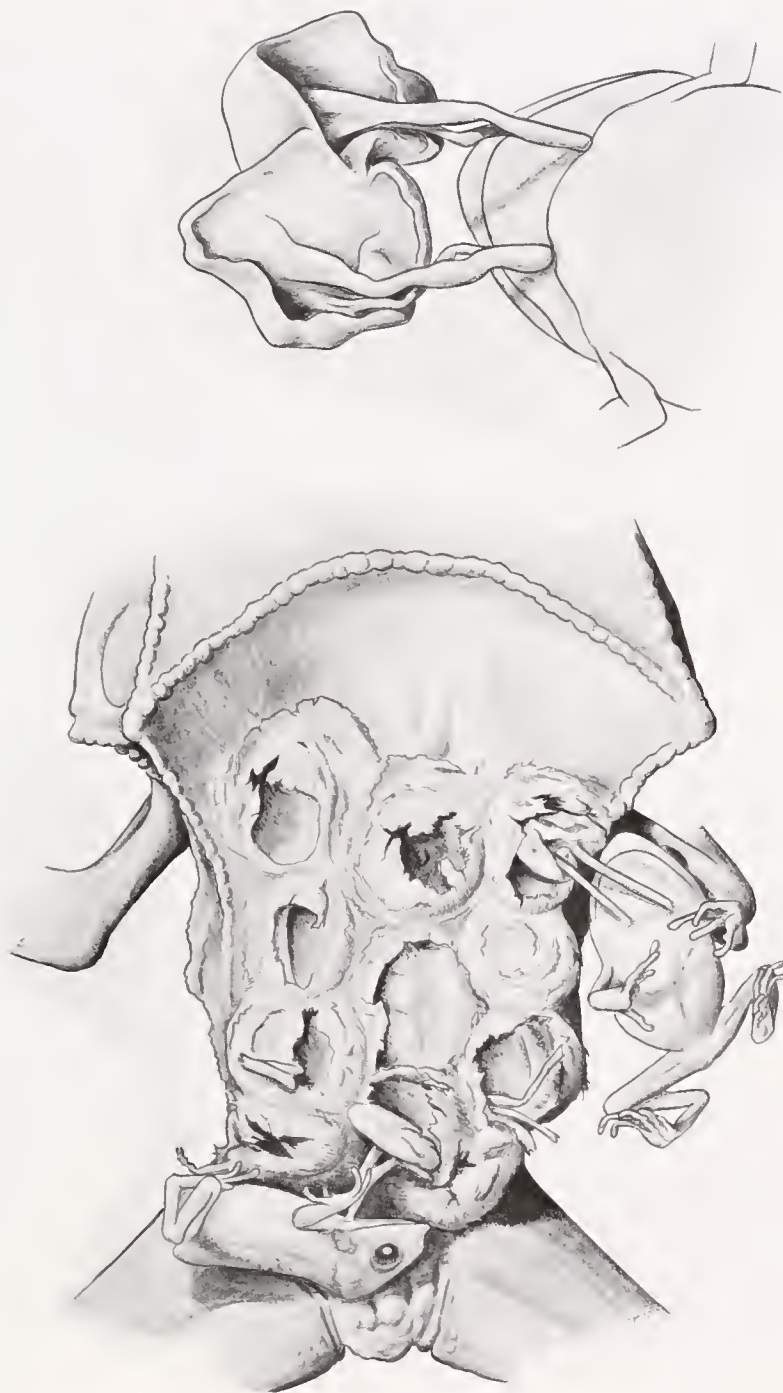




1. *Plectrohyla pycnochila*. 2. *Plectrohyla hartwegi*.  $\times 1.5$ .

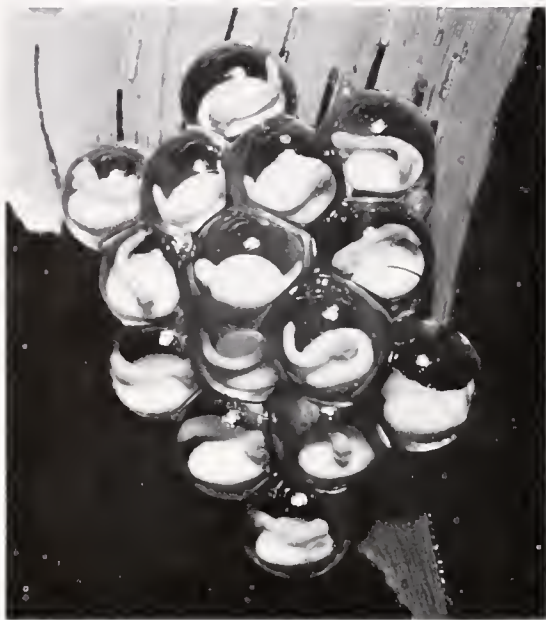


*Hyla miliaria* gliding.  $\times 2$ .



*Hemiphractus panamensis*: 1. "Gills" and cords.  $\times 4$ . 2. Dorsum of female.  $\times 1.5$ .





Egg clutches: 1. *Hyla pseudopuma pseudopuma*. 2. *Hyla lancasteri*. 3. *Hyla bromeliacia*.  
4. *Agalychnis annae*.



*Hyla boans*: 1. Nests at edge of stream. 2. Close-up of one nest.



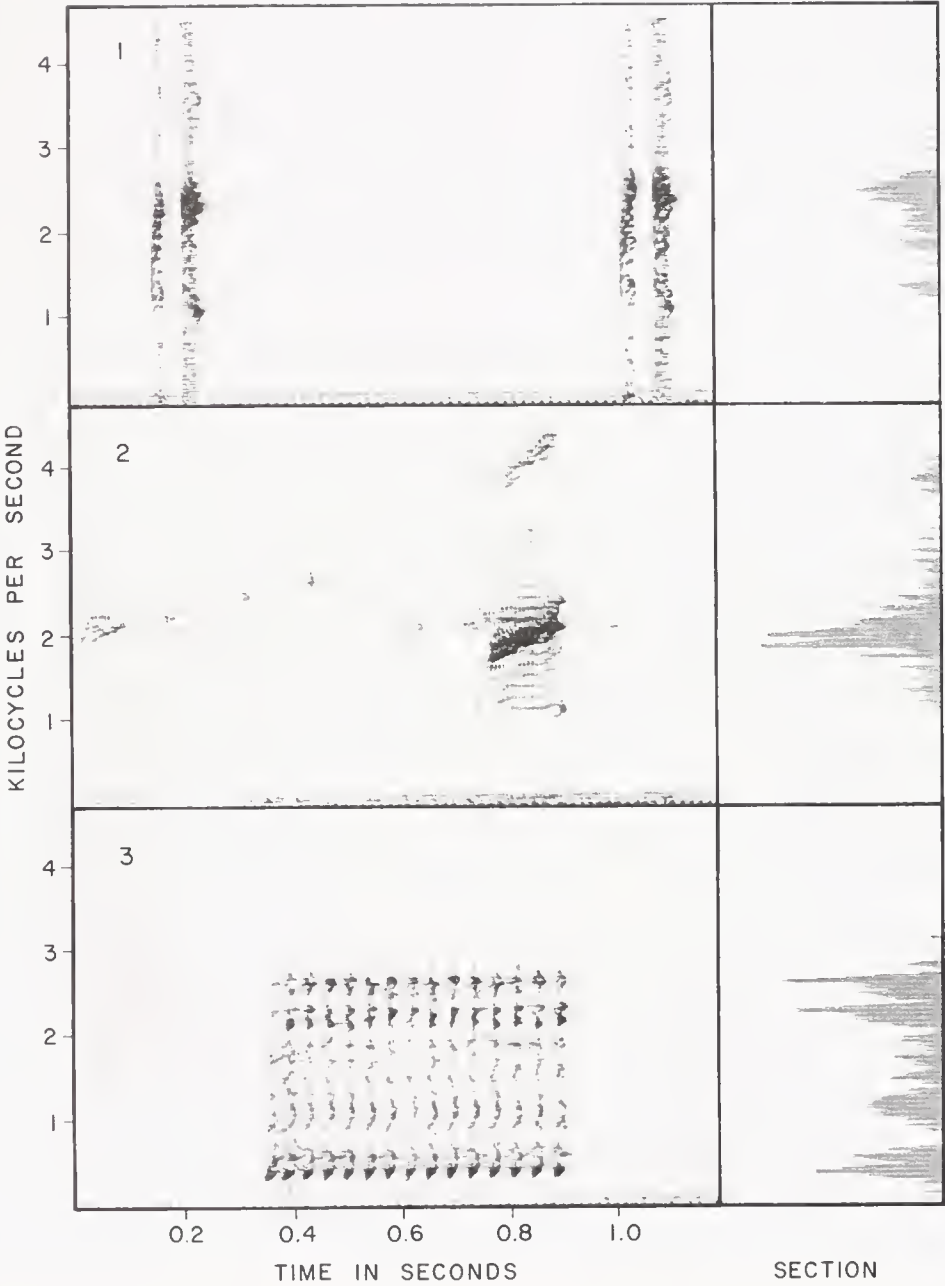


1. Pond at Puerto Viejo, Heredia Province, Costa Rica. 2. Pond at 4 kilometers west-northwest of Esparita, Puntarenas Province, Costa Rica.

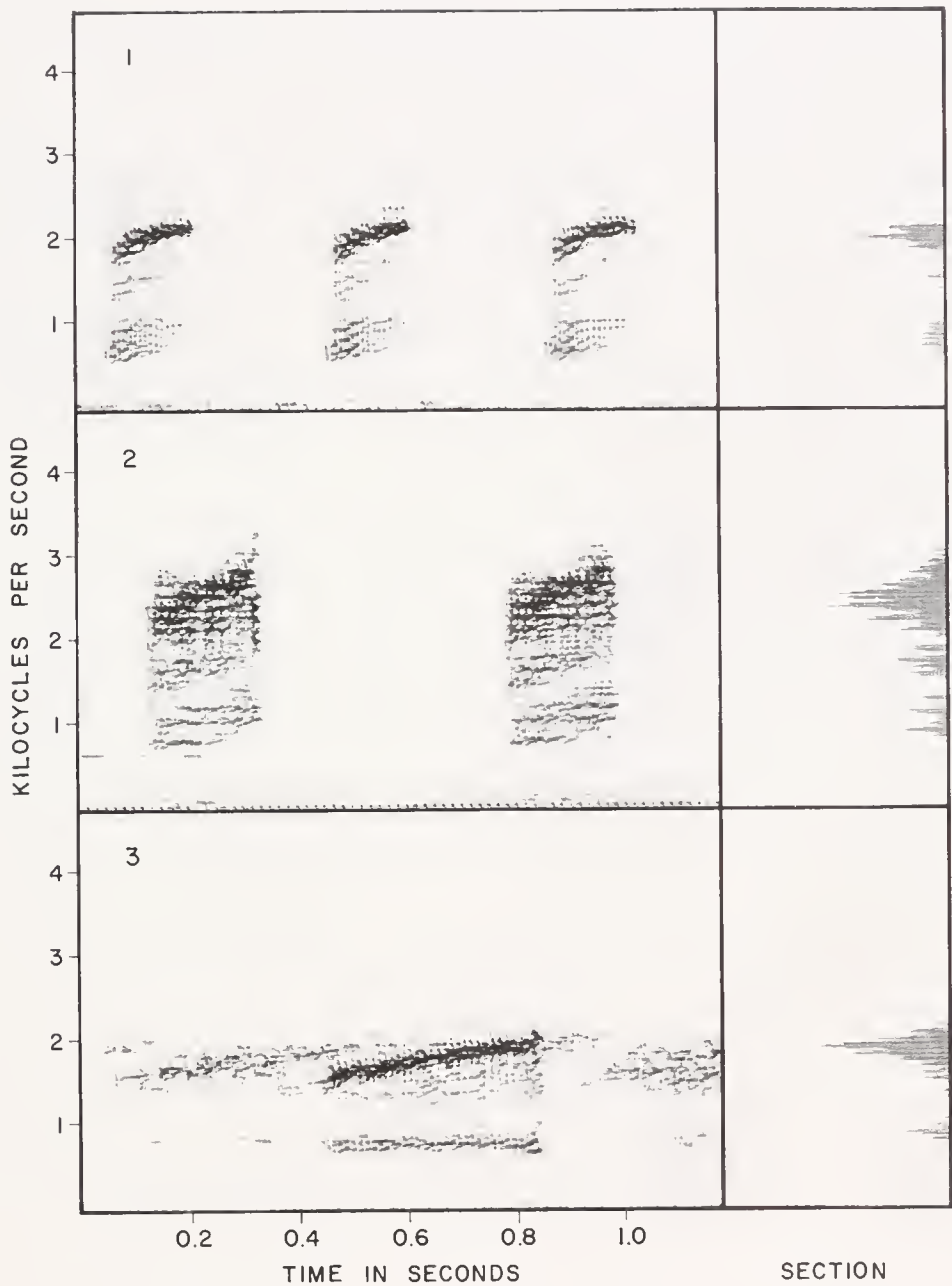




Stream in cloud forest 3 kilometers southwest of Huatusco, Veracruz, México.

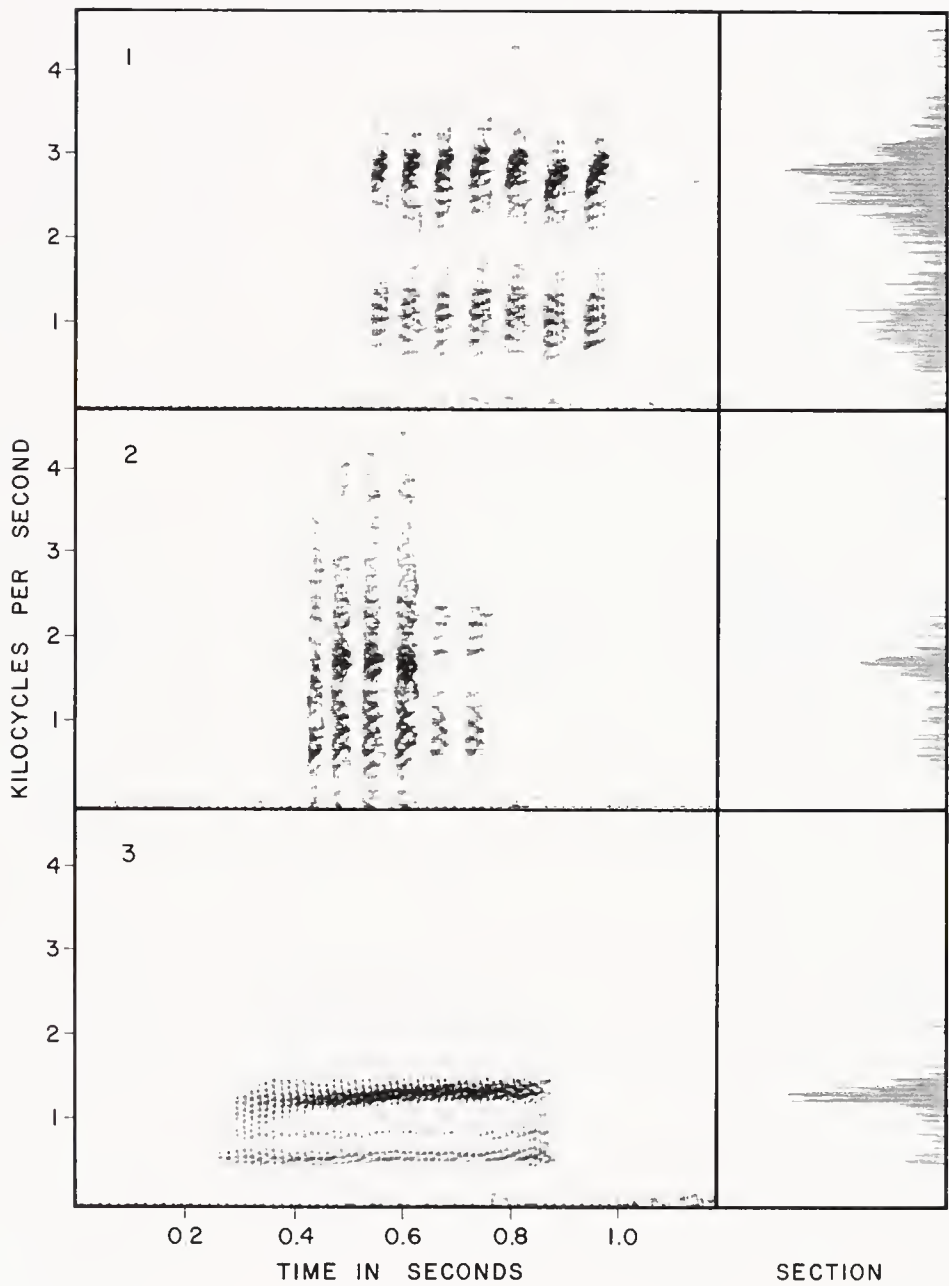


1. *Hyla regilla curta*. 2. *Hyla cadaverina*. 3. *Hyla arenicolor*.

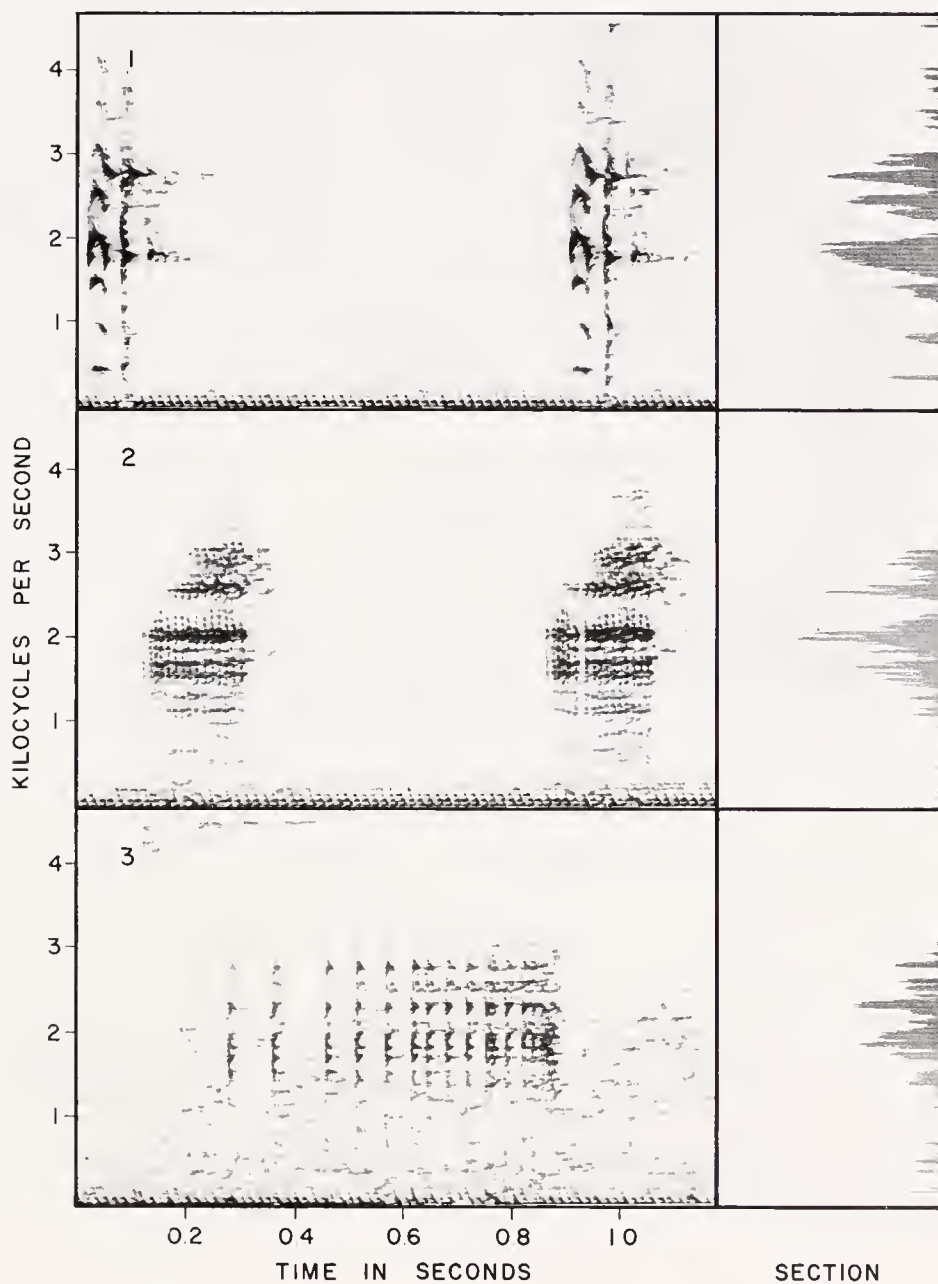


1-3. *Hyla eximia*.

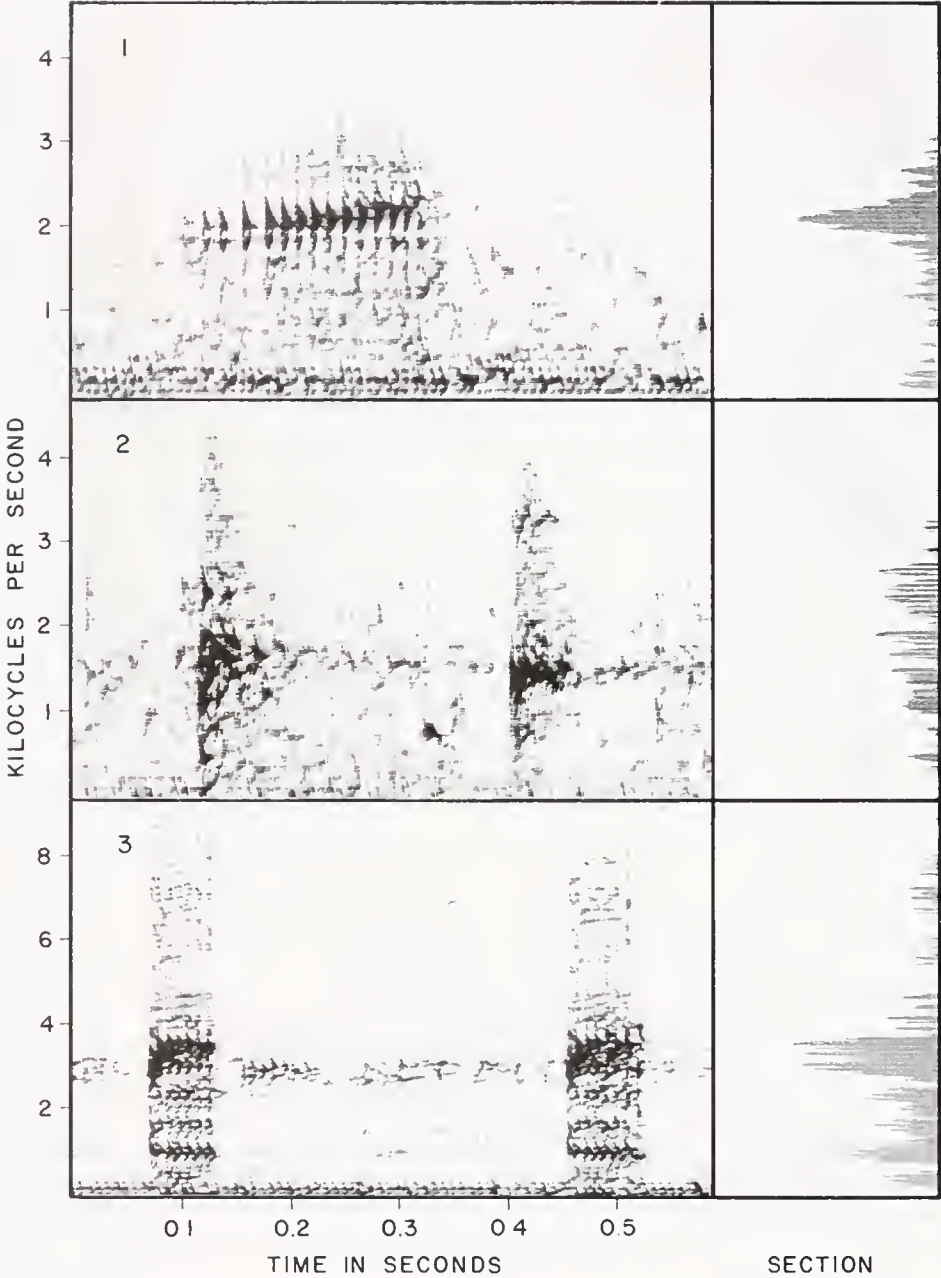




1. *Hyla euphorbiacea*. 2. *Hyla walkeri*. 3. *Hyla plicata*.

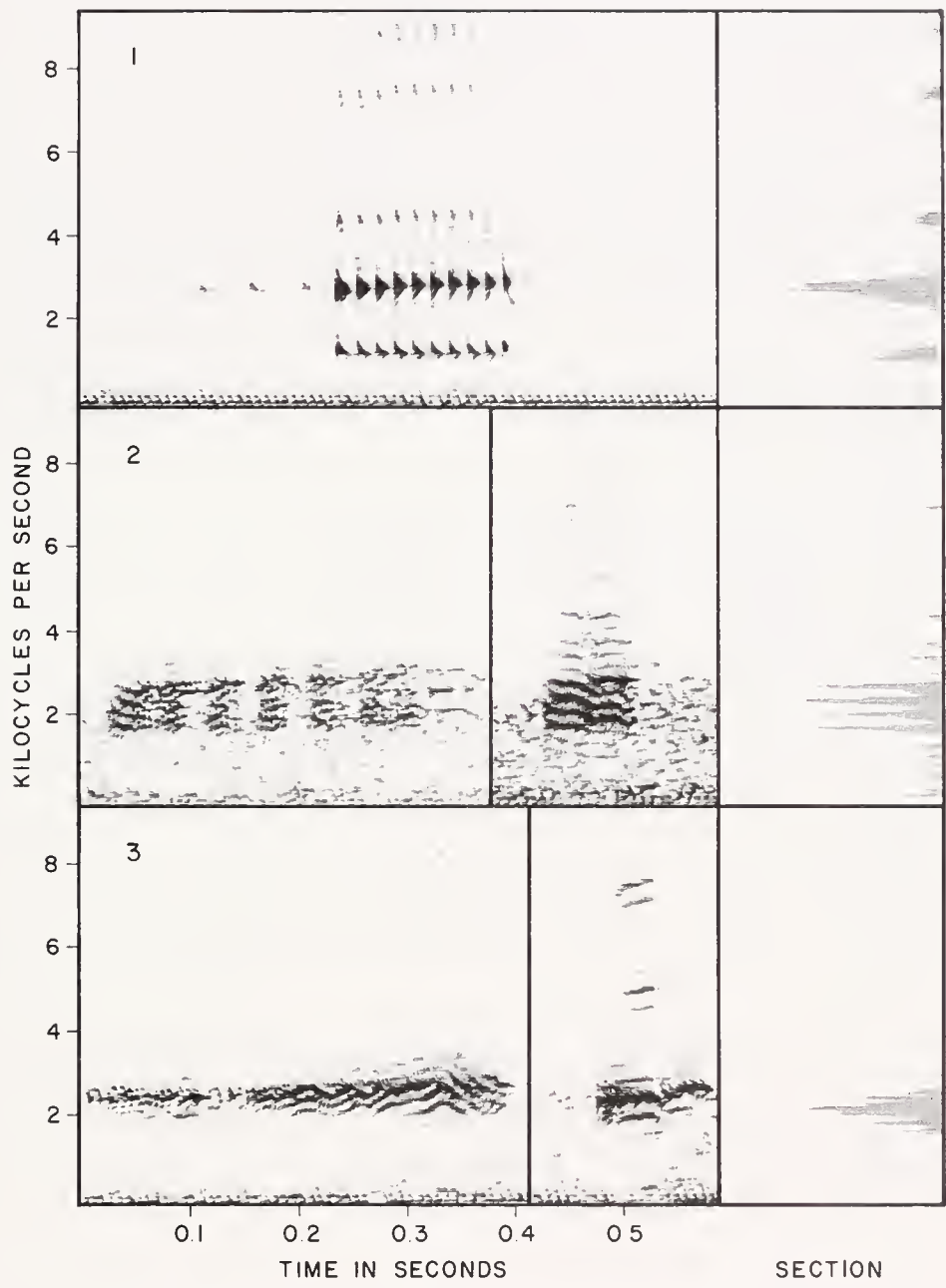


1. *Hyla miotympanum*. 2. *Hyla arborescens*. 3. *Hyla erythromma*.

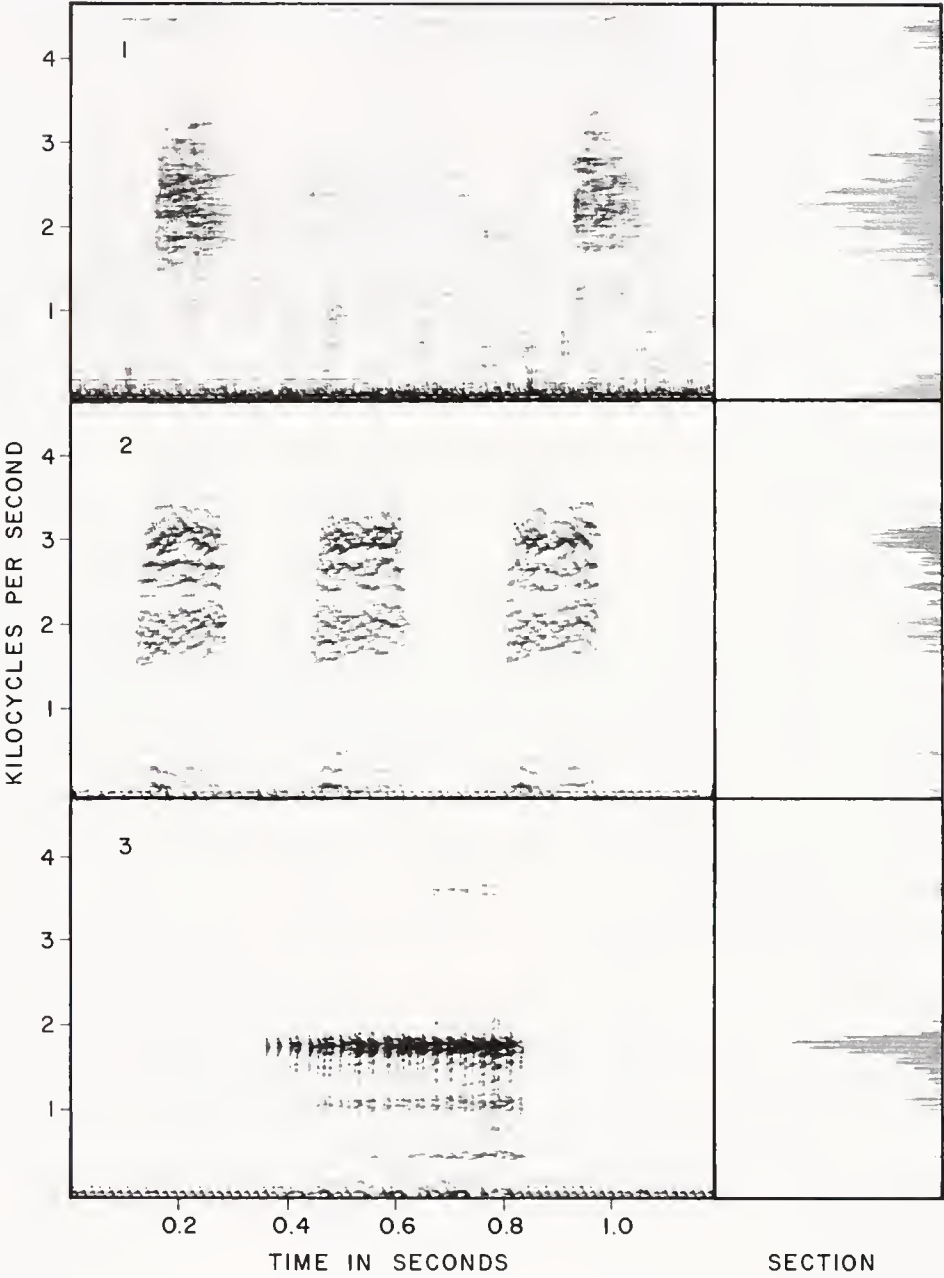


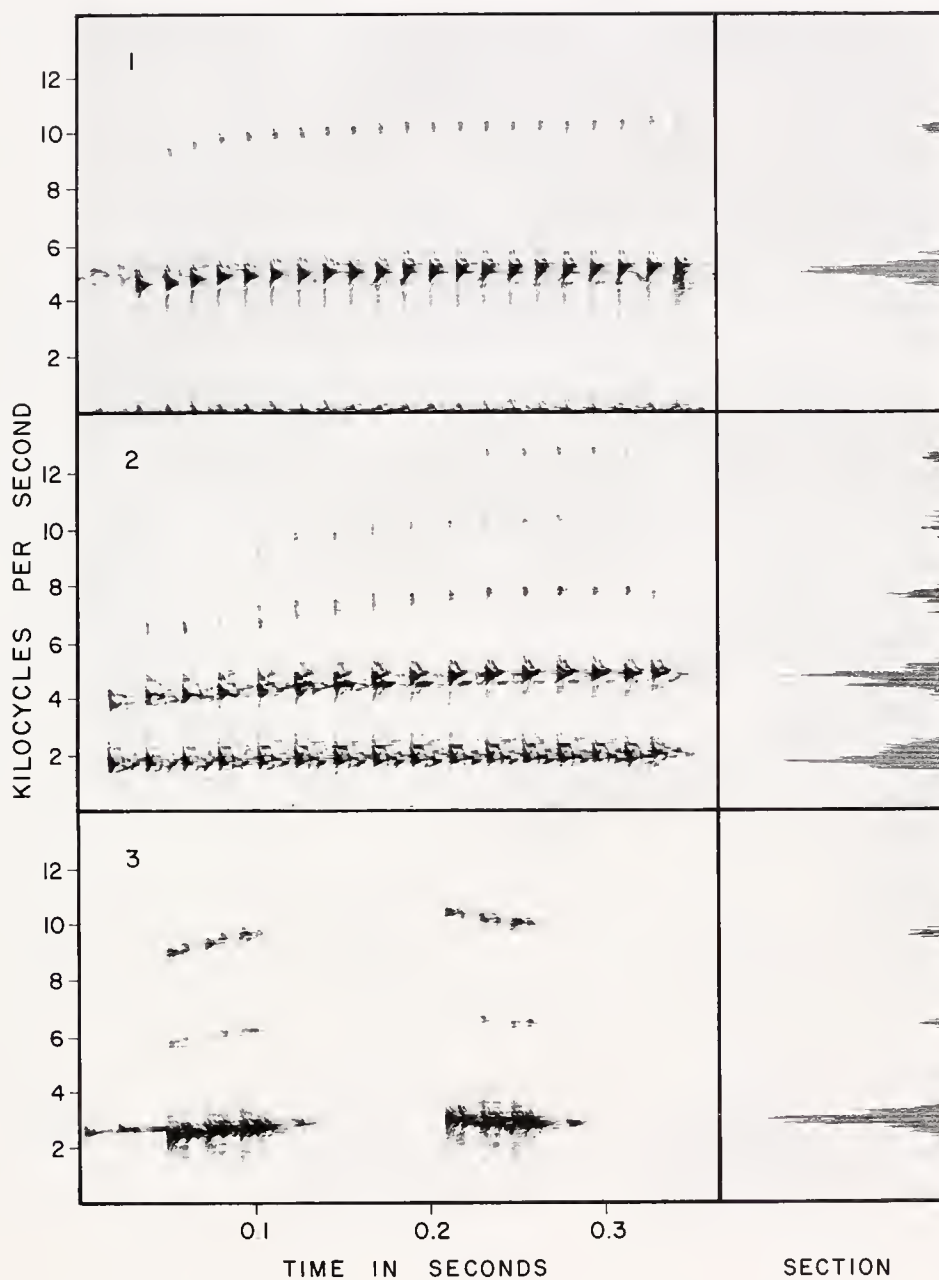
1. *Hyla thorectes*. 2. *Hyla hazelae*. 3. *Hyla loquax*.





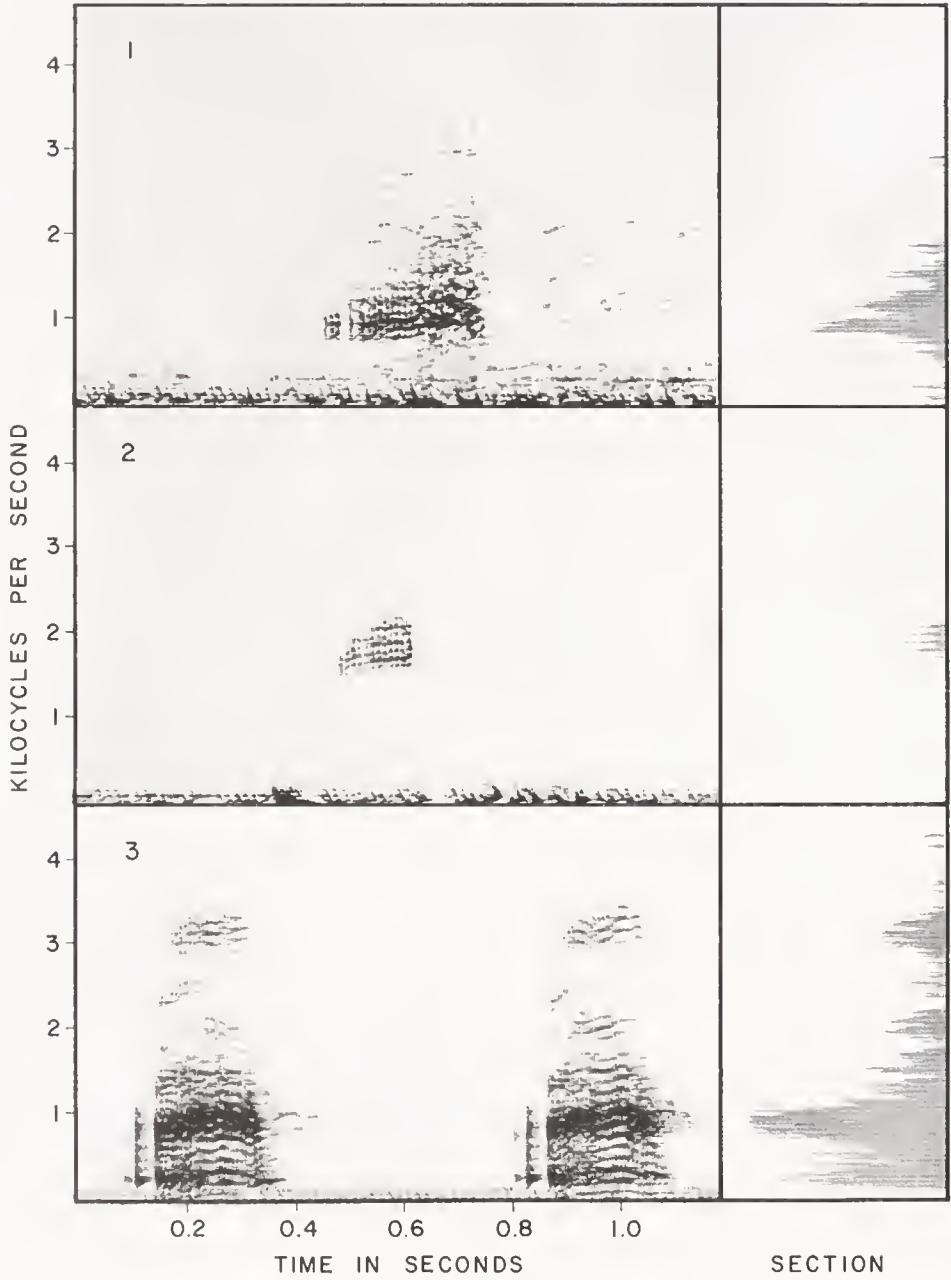
1. *Hyla godmani*. 2. *Hyla melanomma melanomma*. 3. *Hyla melanomma bivocata*.



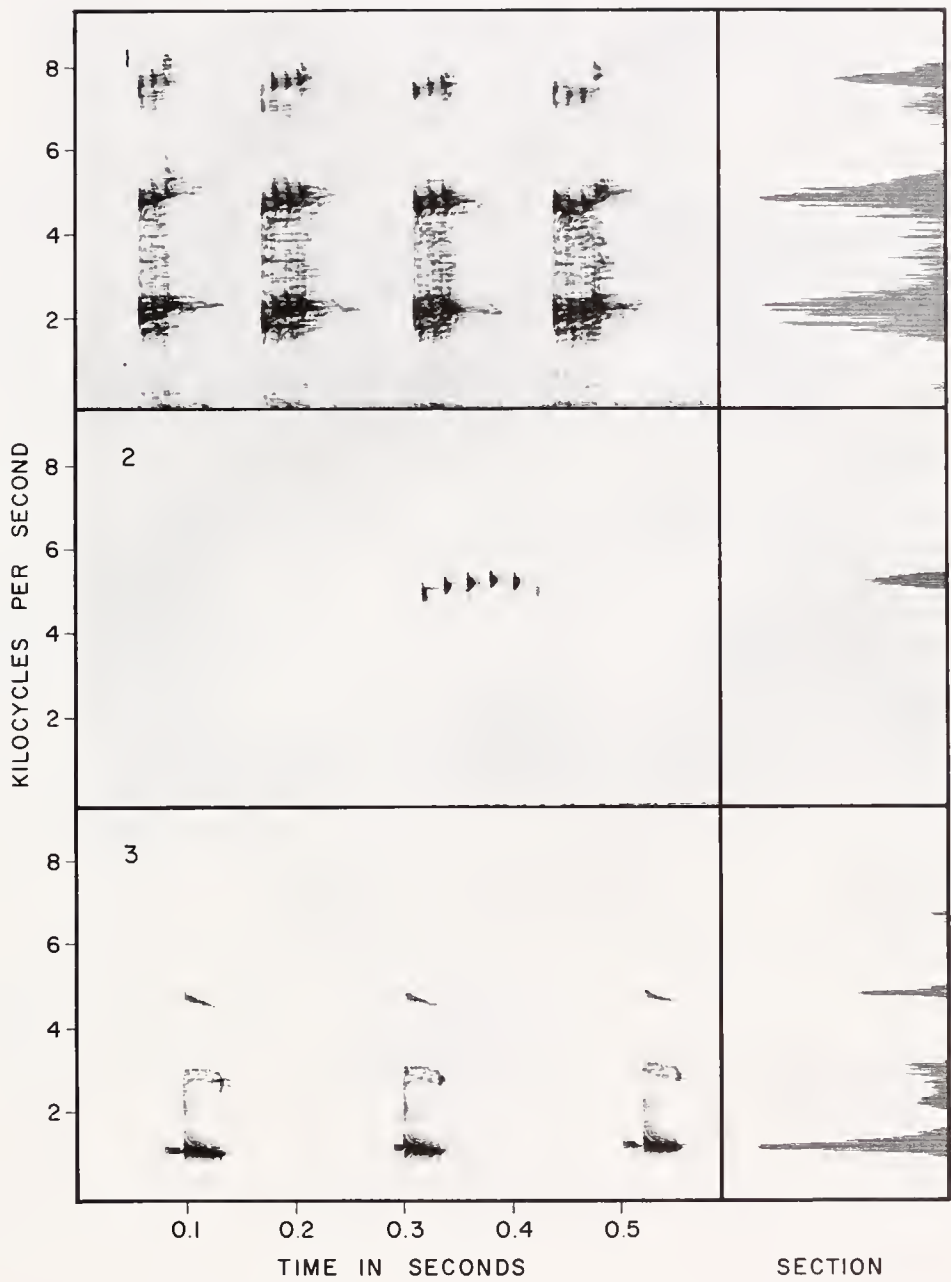


1. *Hyla picta*. 2. *Hyla smithii*. 3. *Hyla rivularis*.

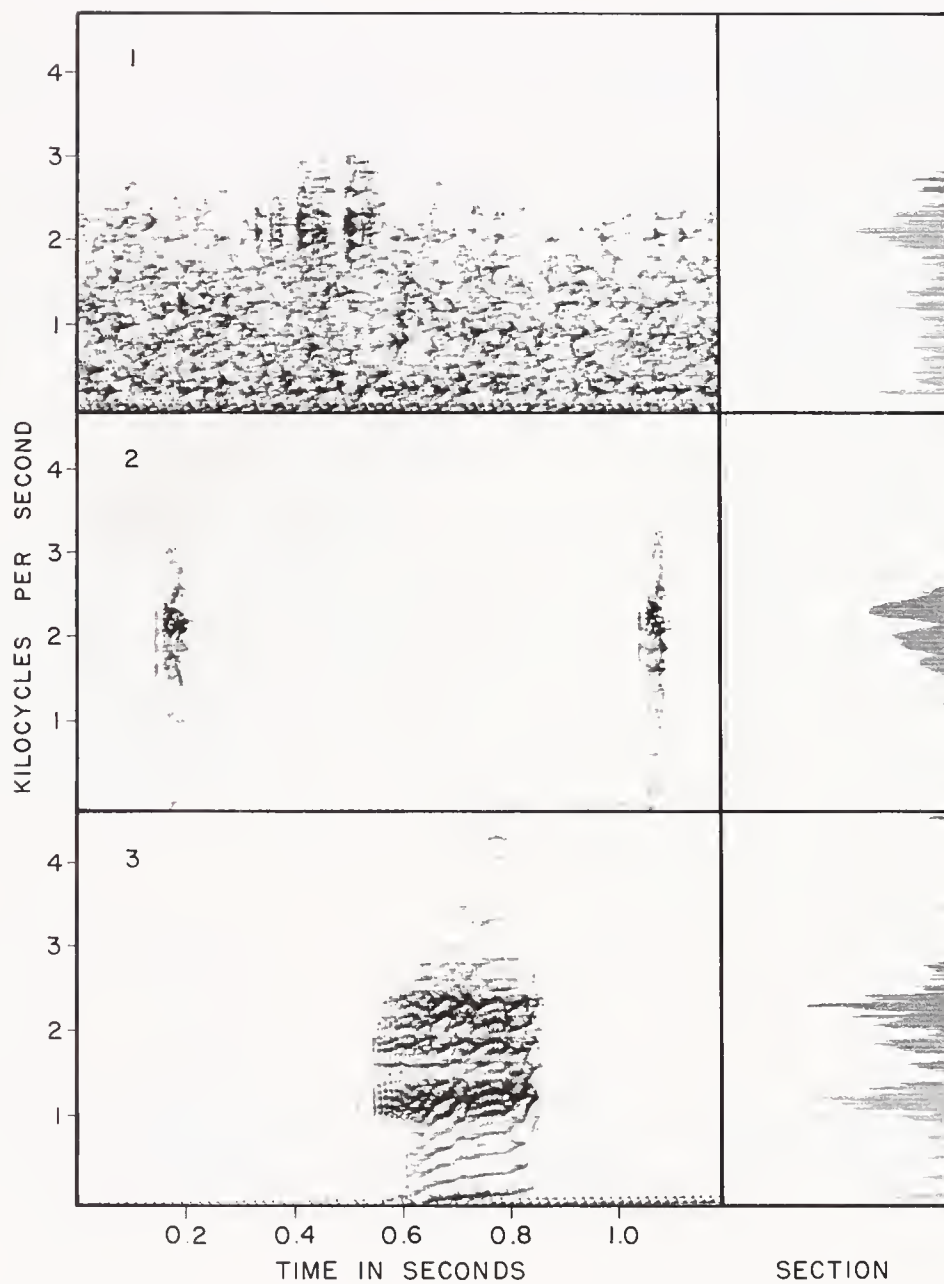




1. *Hyla pseudopuma pseudopuma*. 2. *Hyla angustilineata*. 3. *Hyla boans*.

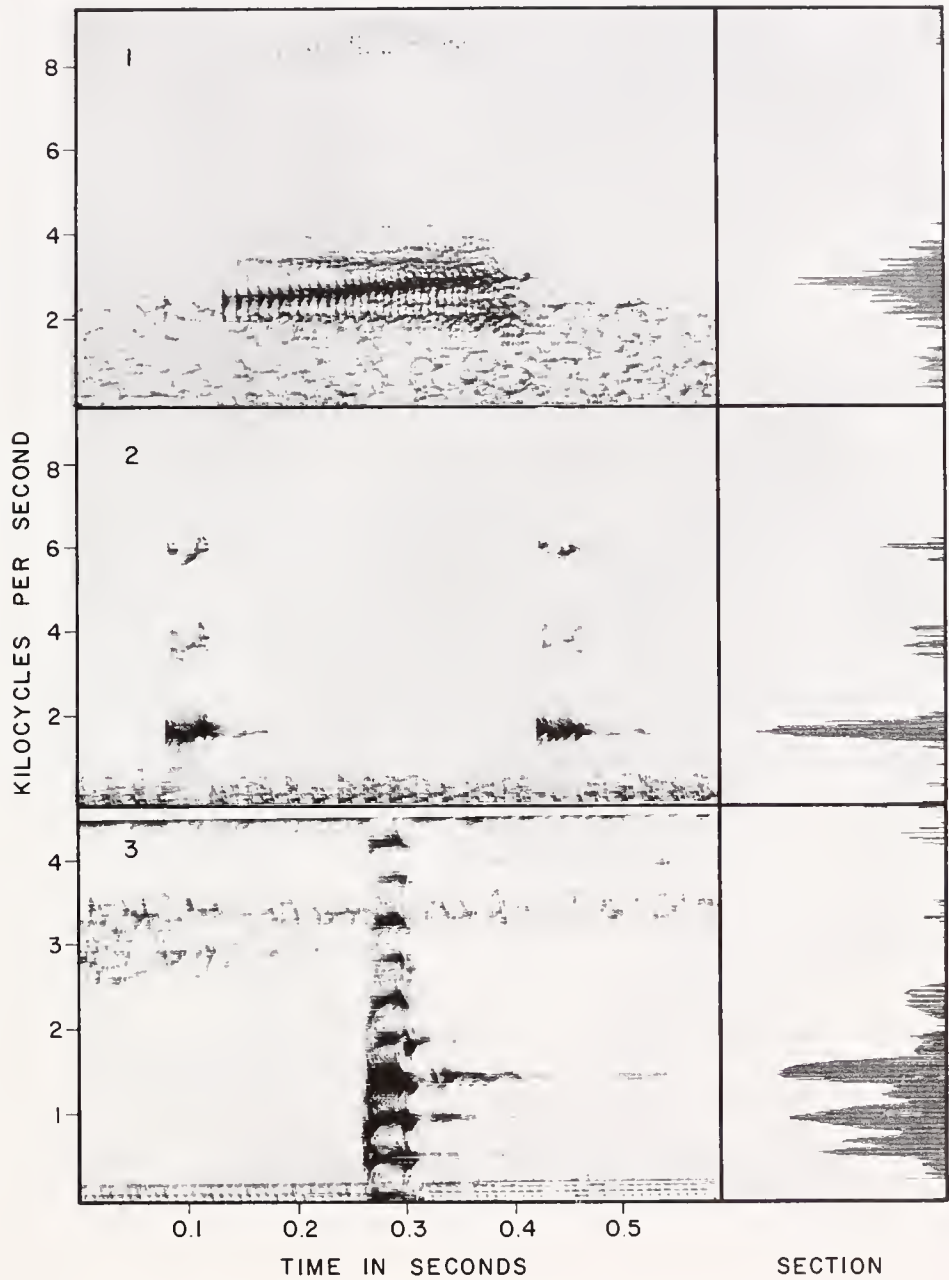


1. *Hyla tica*. 2. *Hyla debilis*. 3. *Hyla uranochroa*.

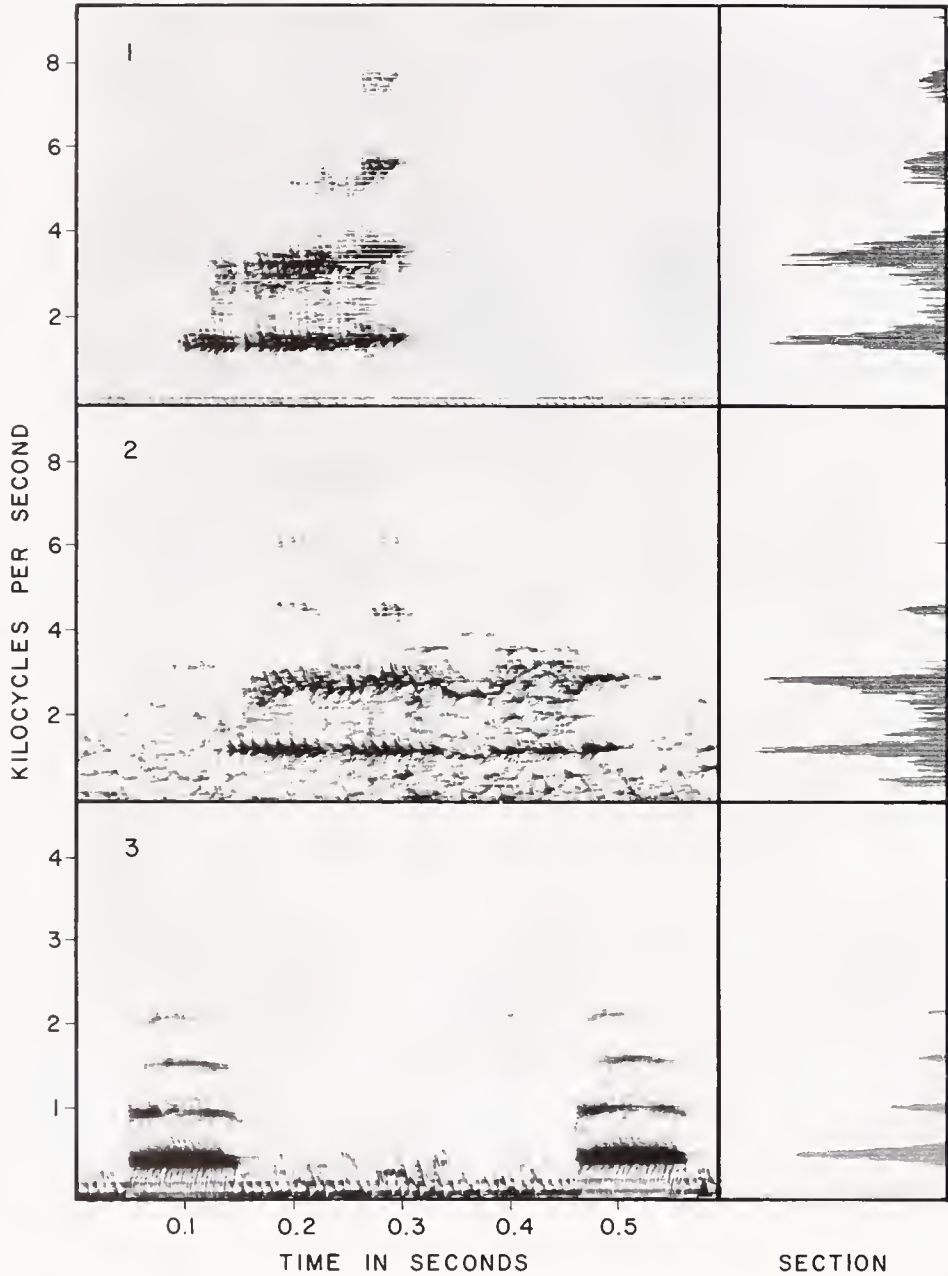


1. *Hyla rufoculis*. 2. *Hyla salvadorensis*. 3. *Hyla legleri*.

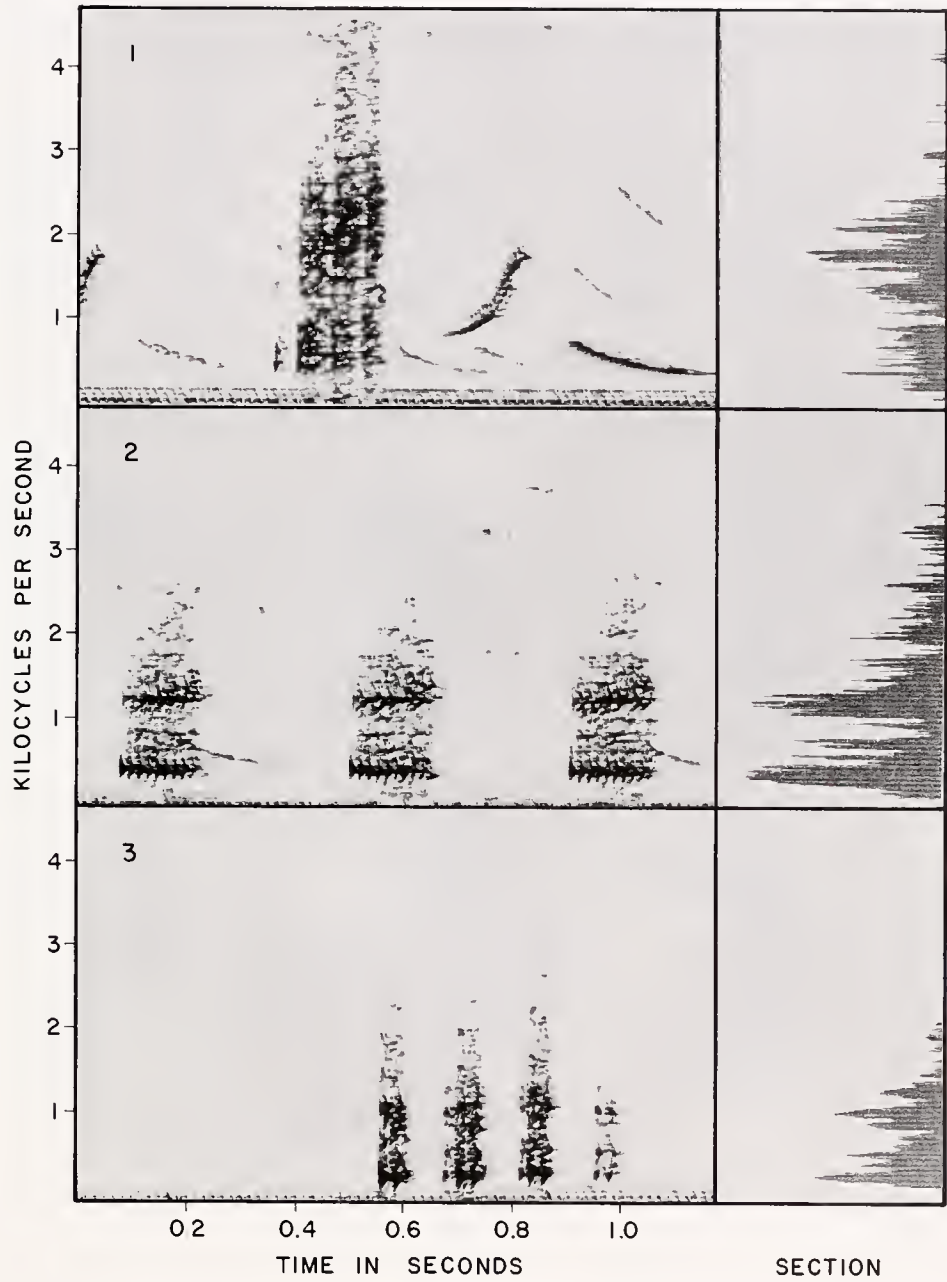




1. *Hyla pictipes*. 2. *Hyla colymba*. 3. *Hyla rufitela*.

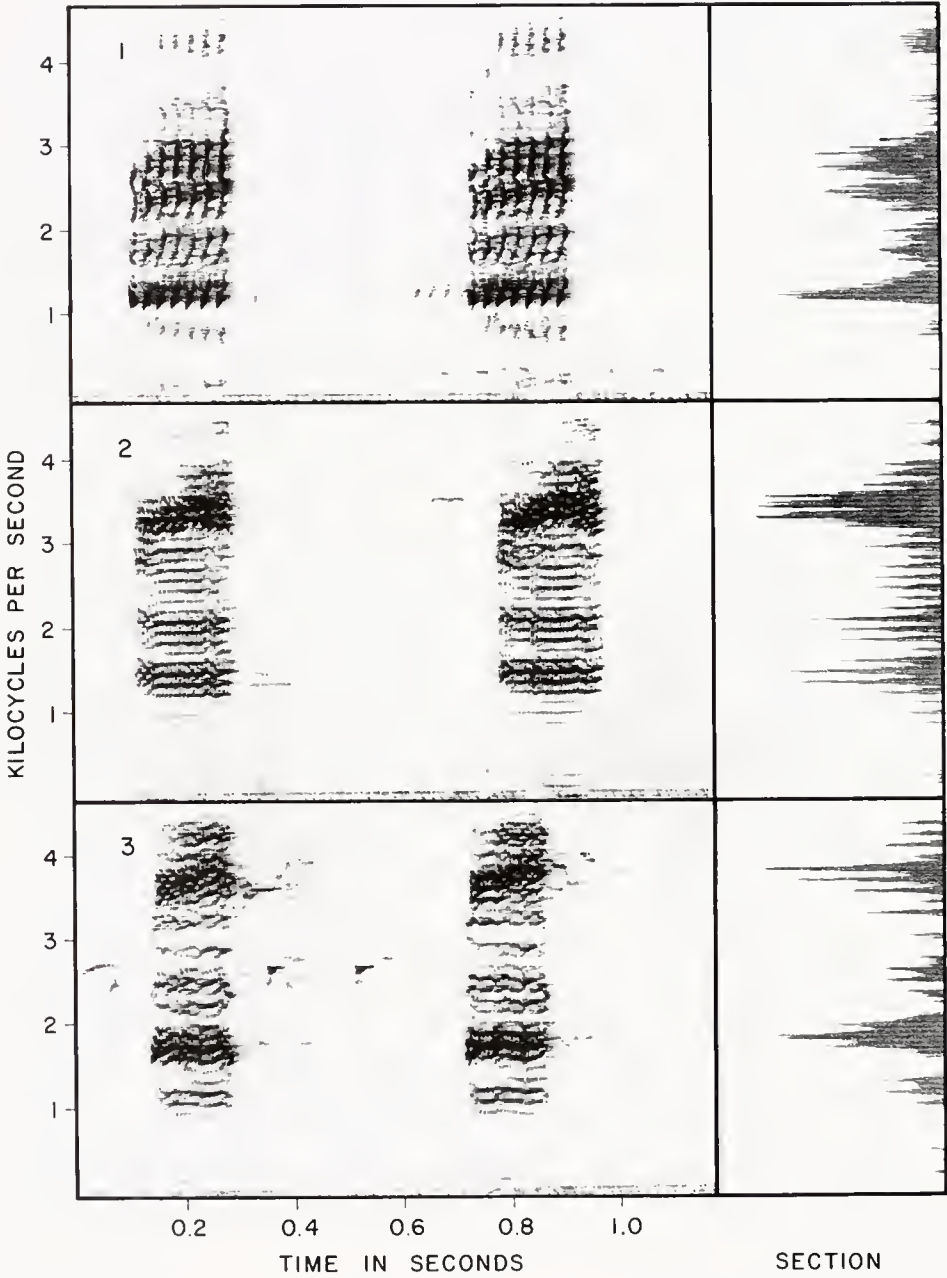


1 and 2. *Hyla lancasteri*. 3. *Anothea spinosa*.

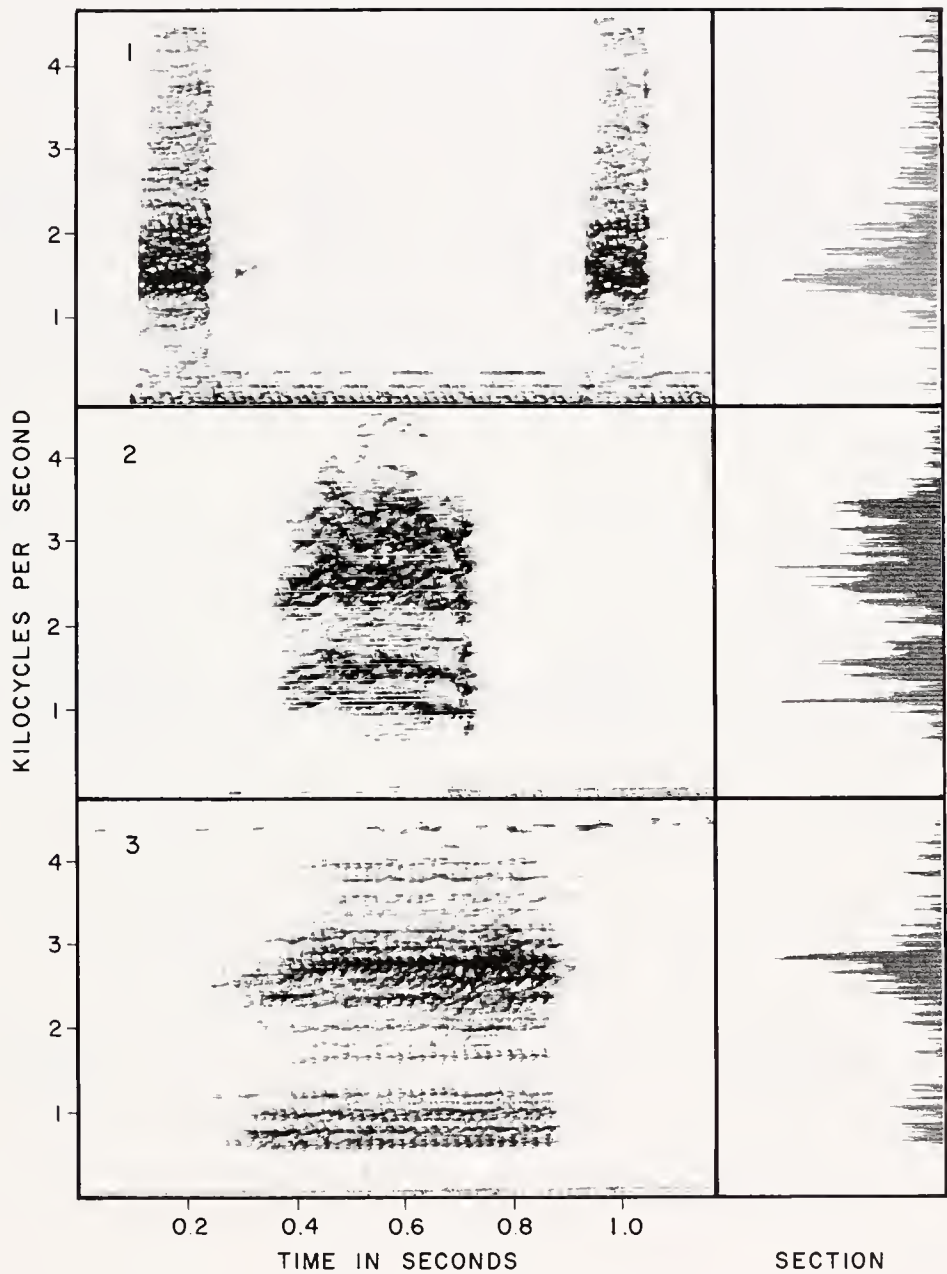


1. *Hyla crepitans*. 2. *Hyla crepitans*  $\times$  *rosenbergi*. 3. *Hyla rosenbergi*.

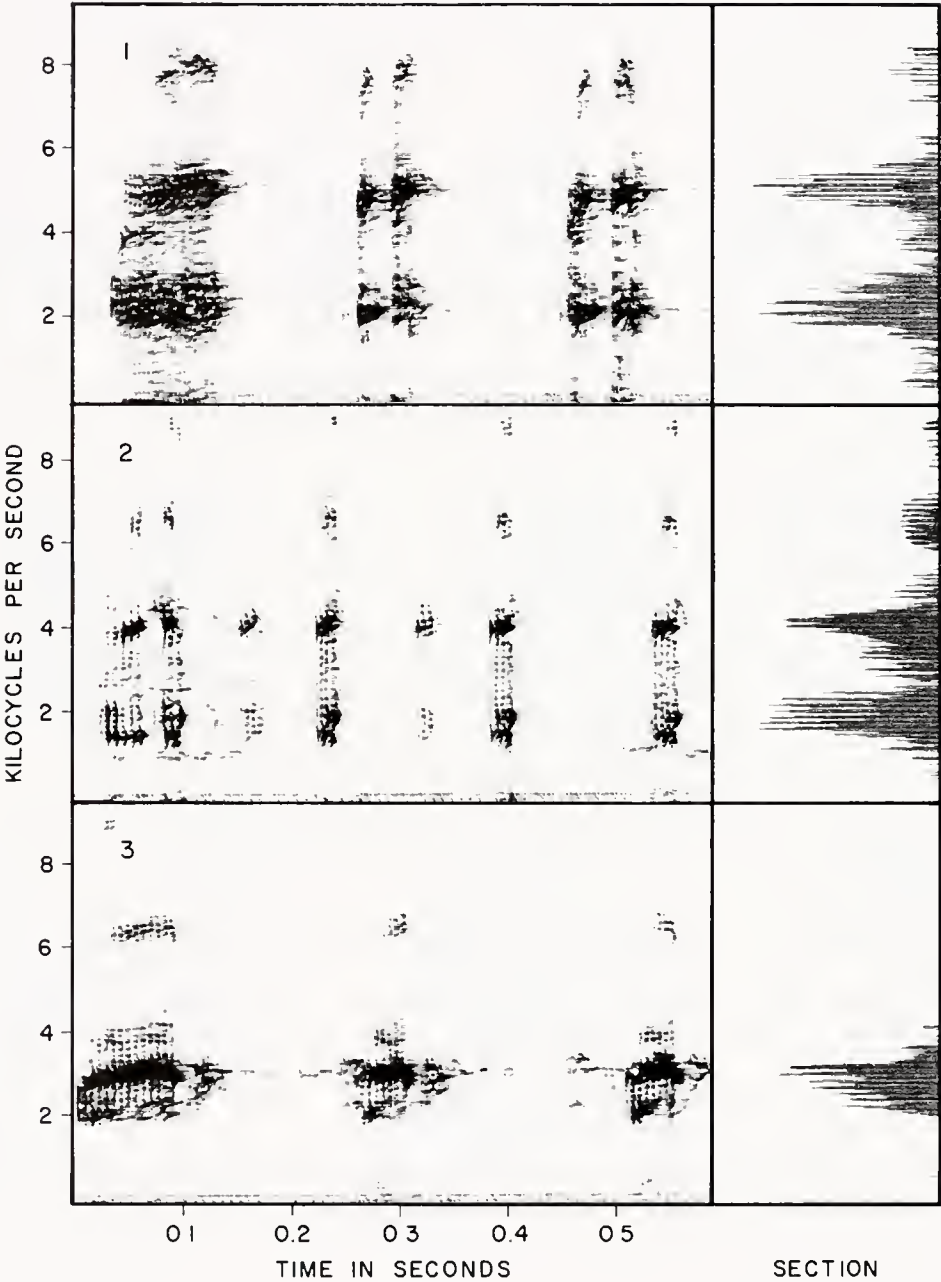




1. *Hyla elaeochroa*. 2. *Hyla staufferi staufferi*. 3. *Hyla staufferi altae*.

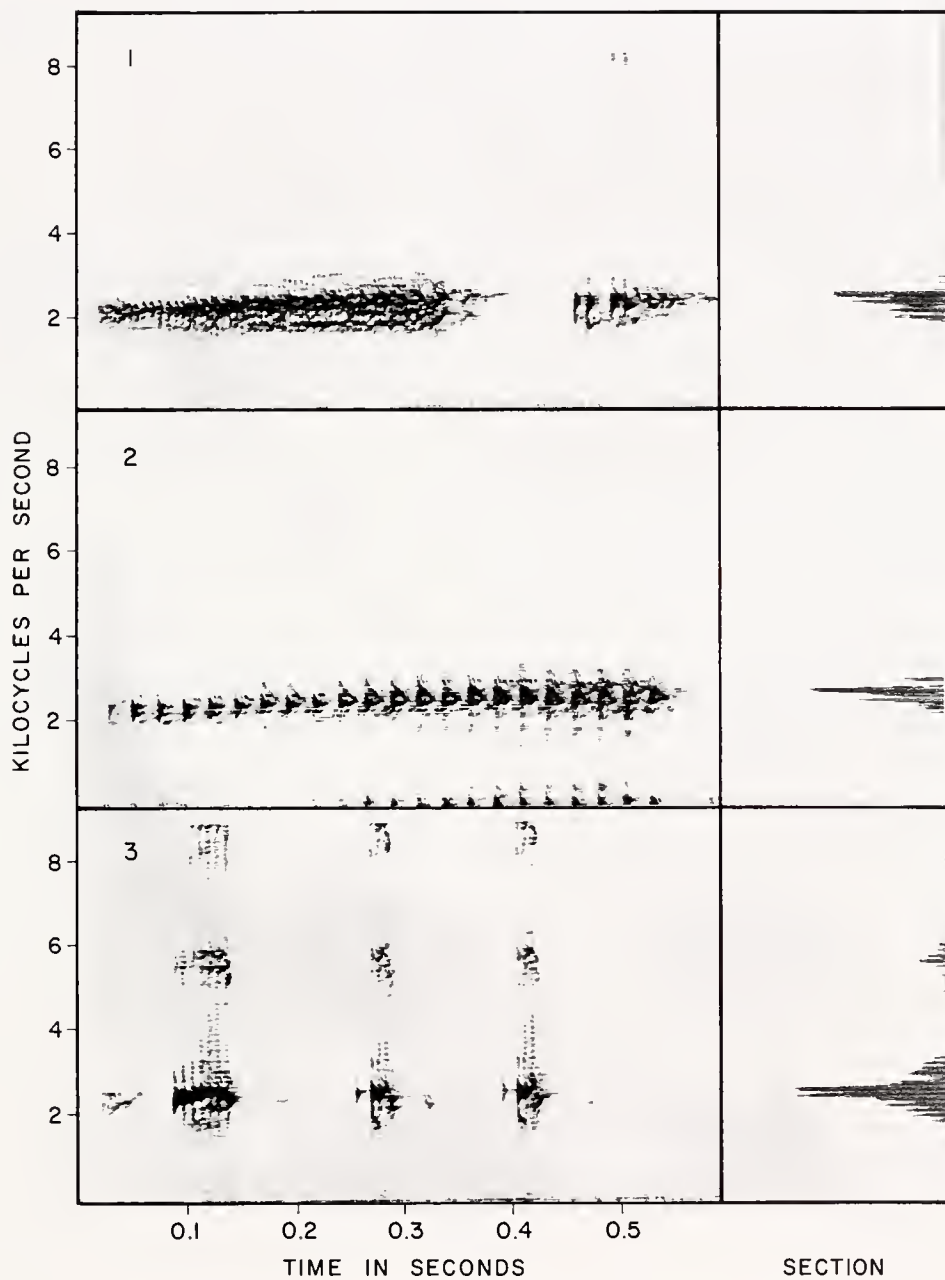


1. *Hyla rubra*. 2. *Hyla boulengeri*. 3. *Hyla rostrata*.

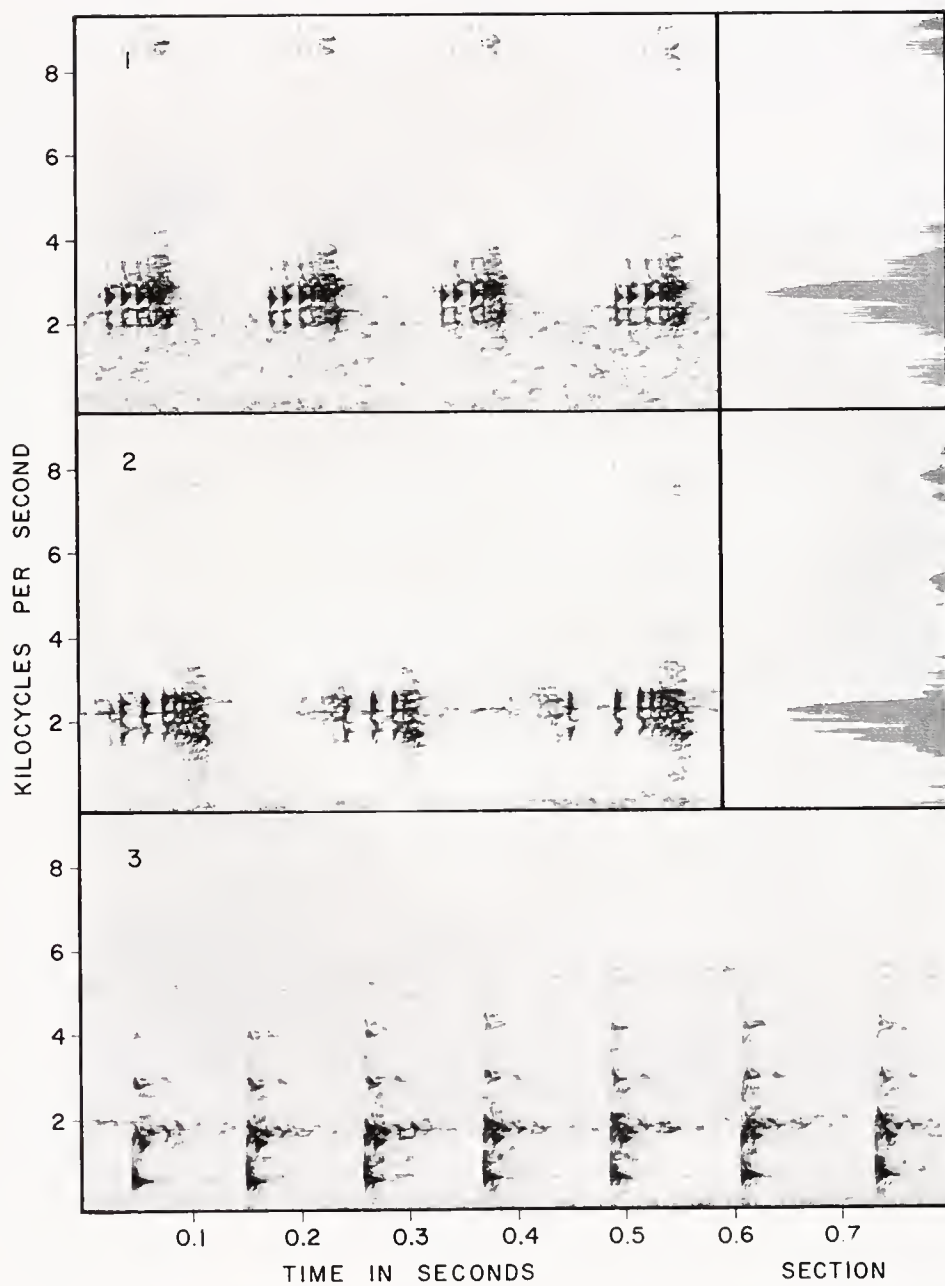


1. *Hyla microcephala microcephala*. 2. *Hyla phlebodes*. 3. *Hyla robertmertensi*.

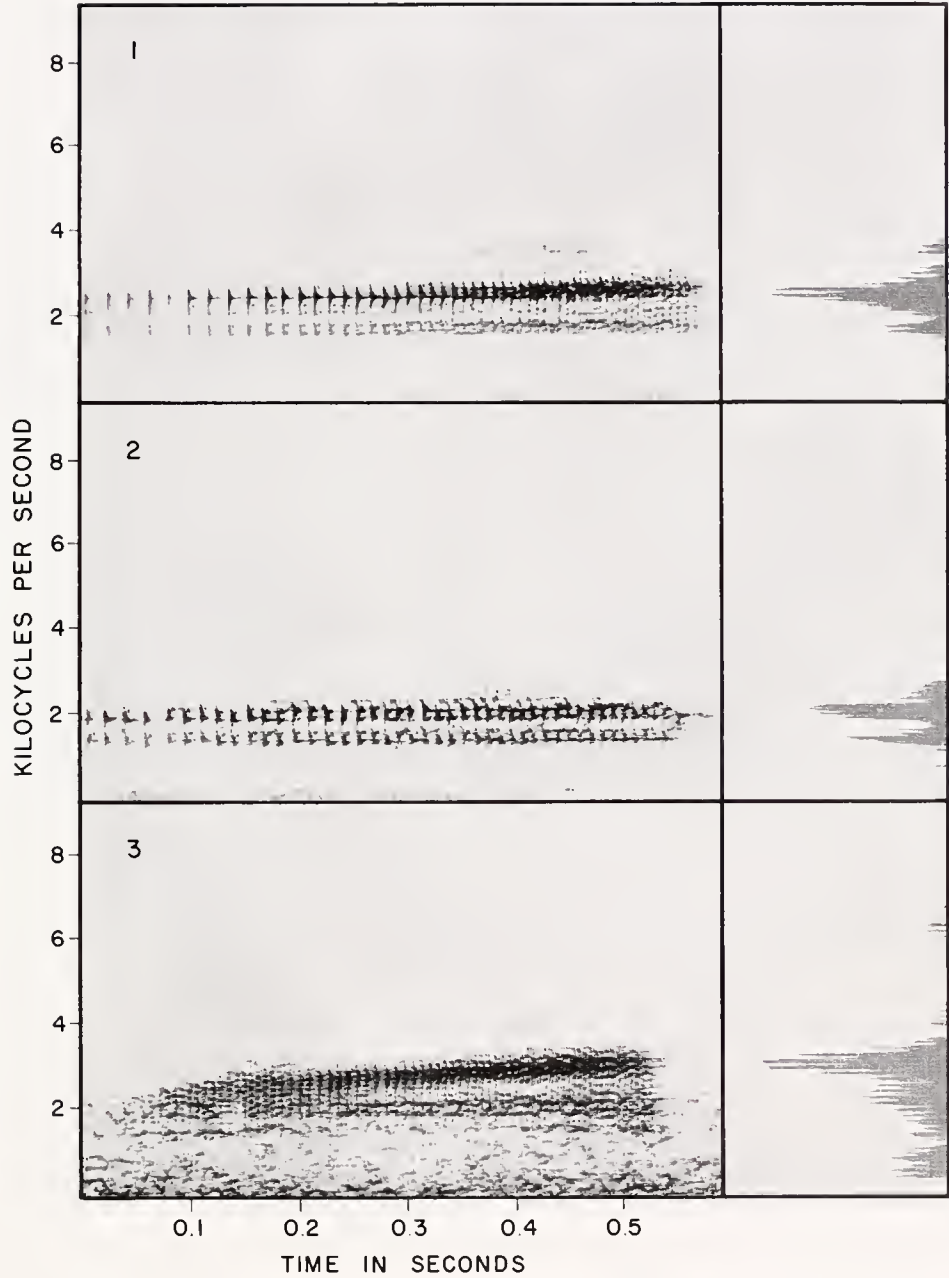




1. *Hyla ebraccata*. 2. *Hyla subocularis*. 3. *Hyla sartori*.

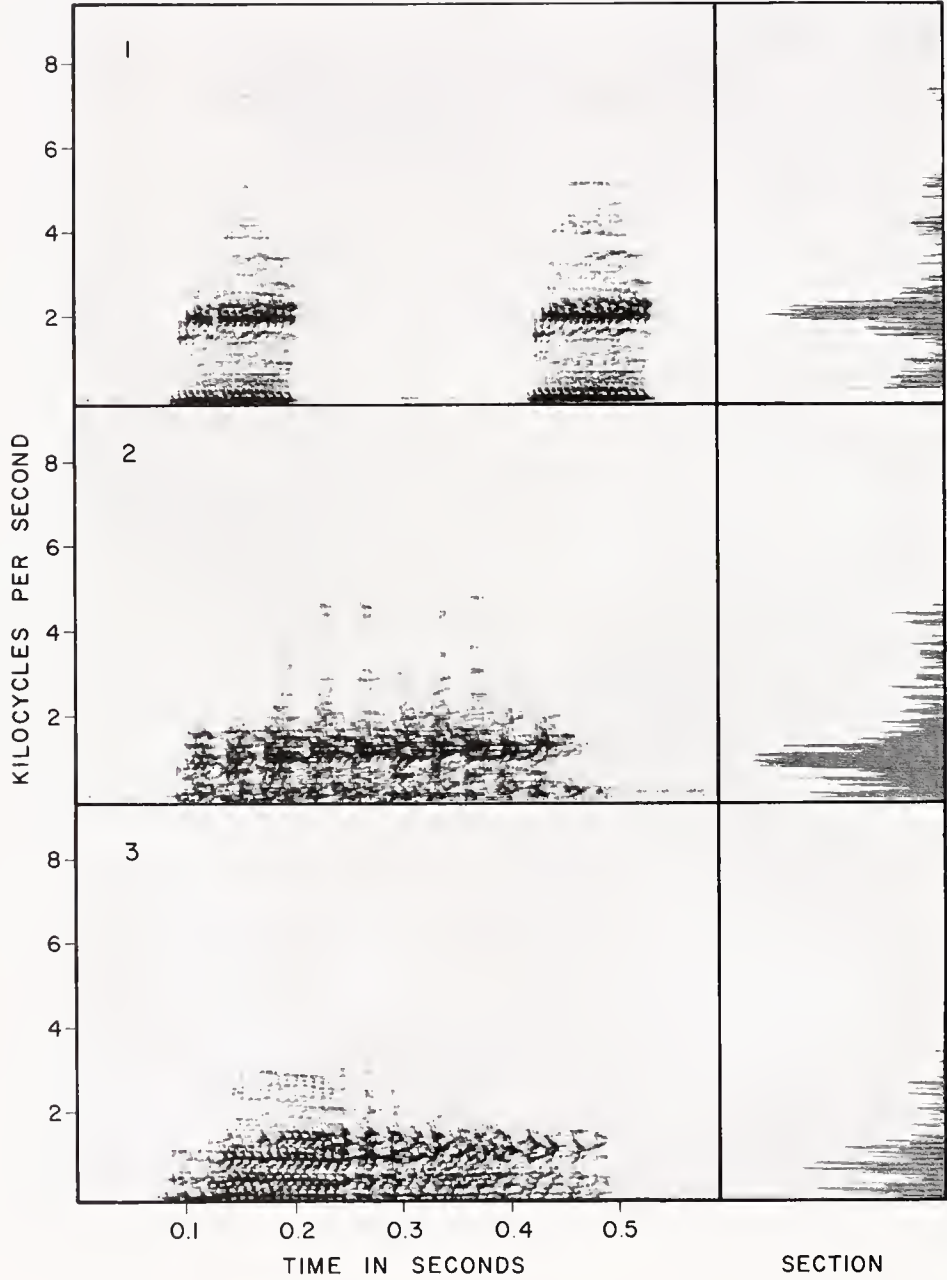


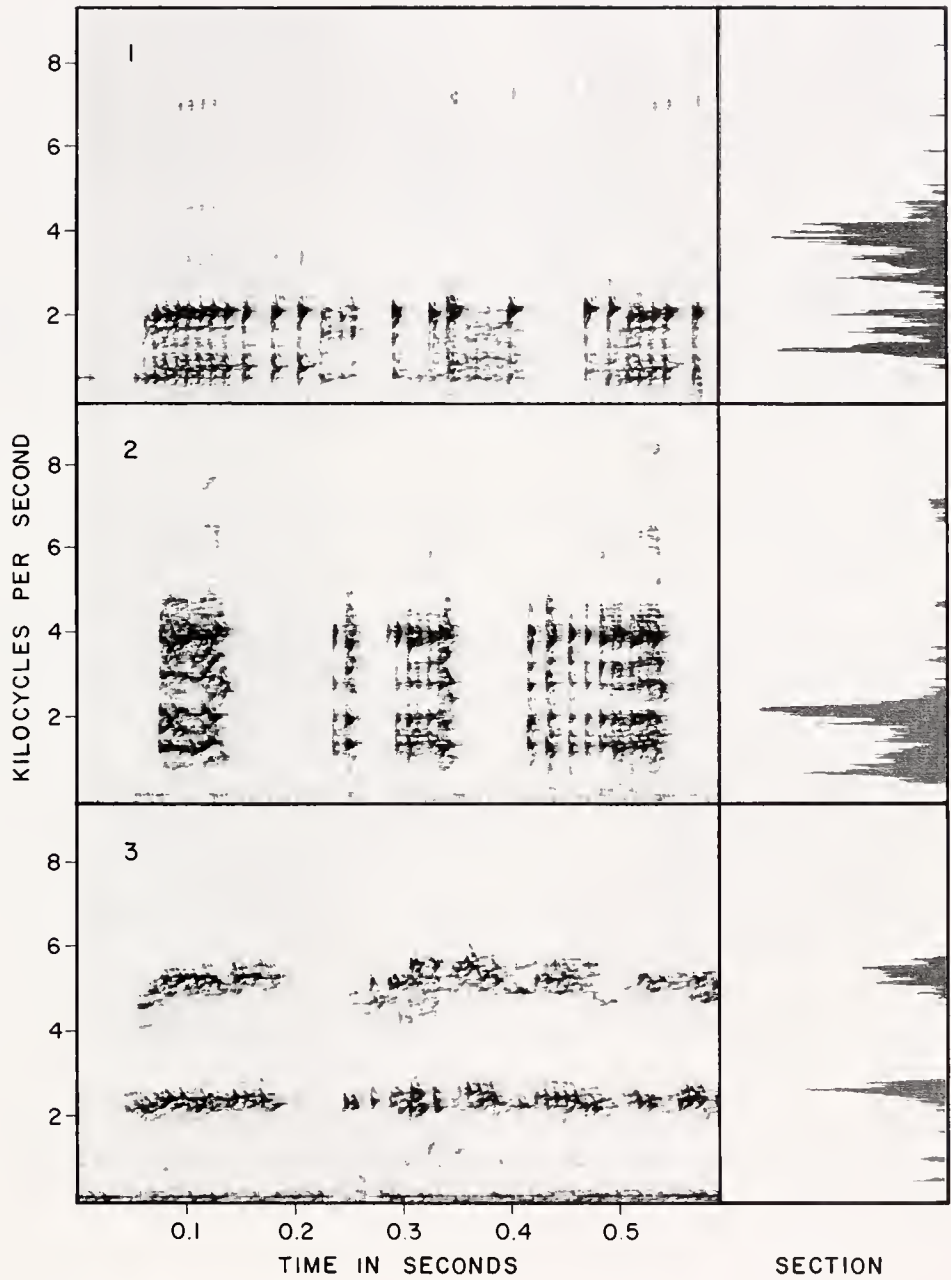
1. *Ptychohyla schmidtorum chamulae*. 2. *Ptychohyla ignicolor*. 3. *Agalychnis callidryas* (rain call).



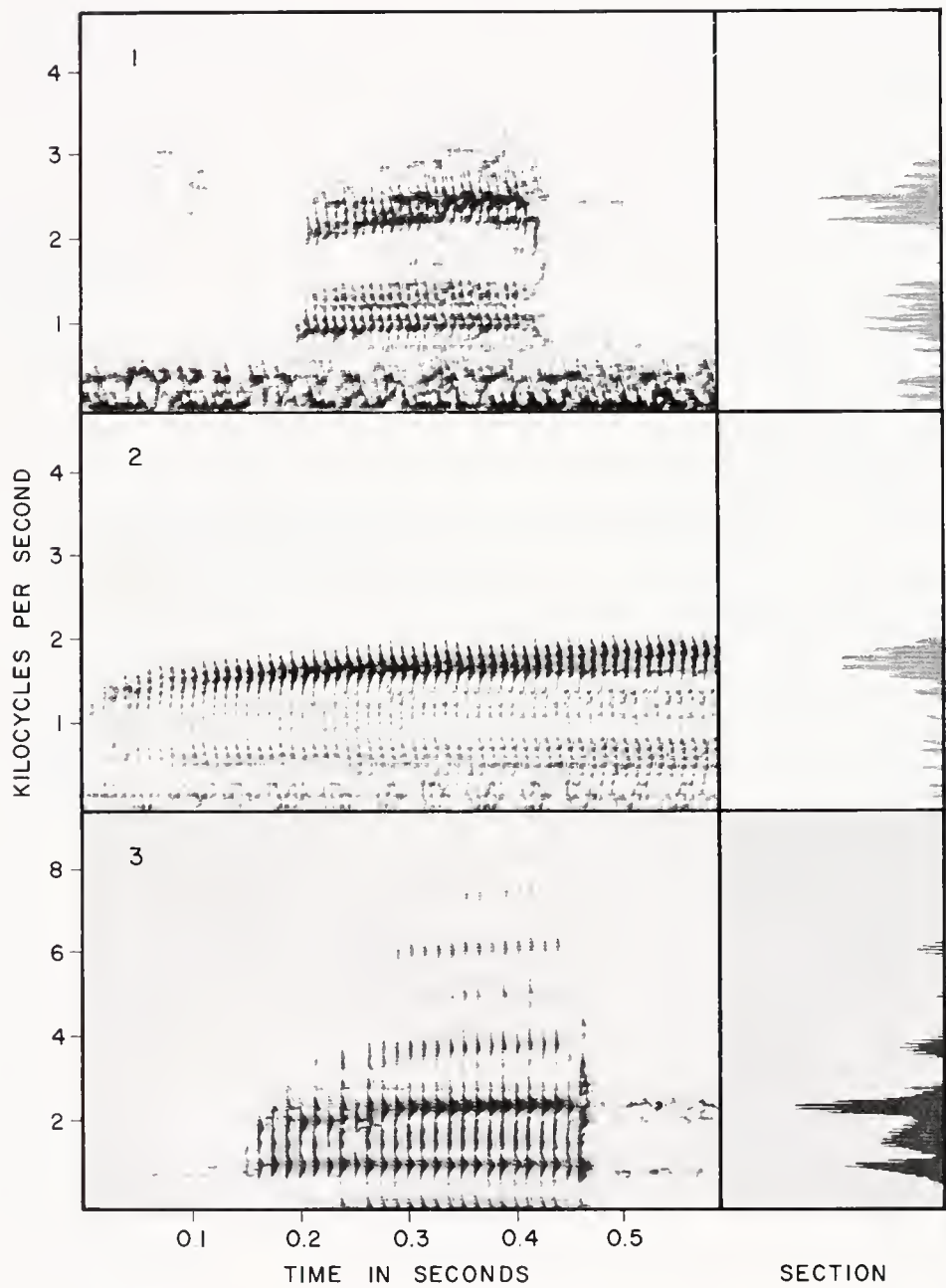
1. *Ptychohylla euthysanota macrotympanum*. 2. *Ptychohylla leonhardschultzei*. 3. *Ptychohylla spinipollex*.





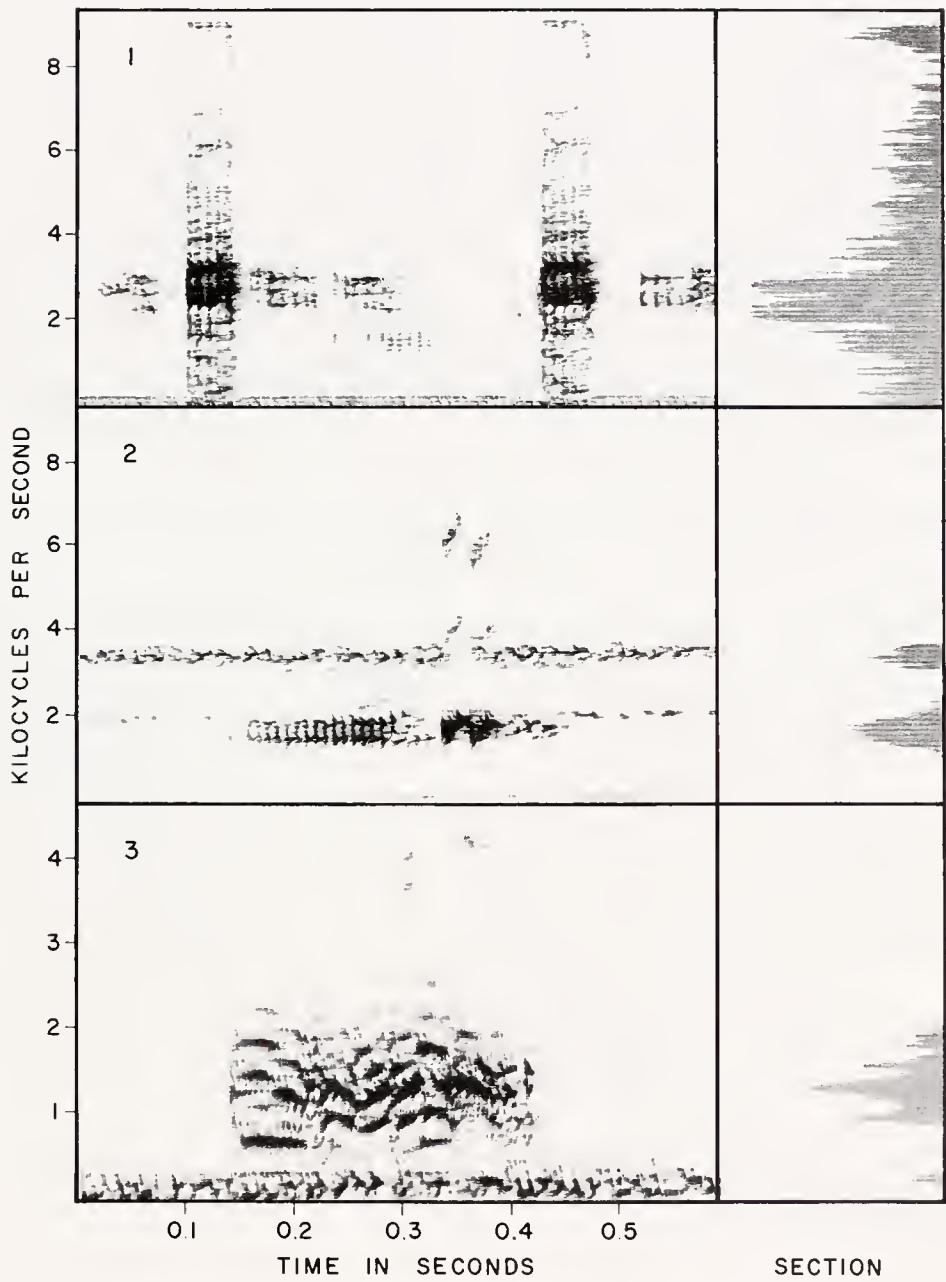


1. *Smilisca puma*. 2. *Smilisca sila*. 3. *Smilisca sordida*.

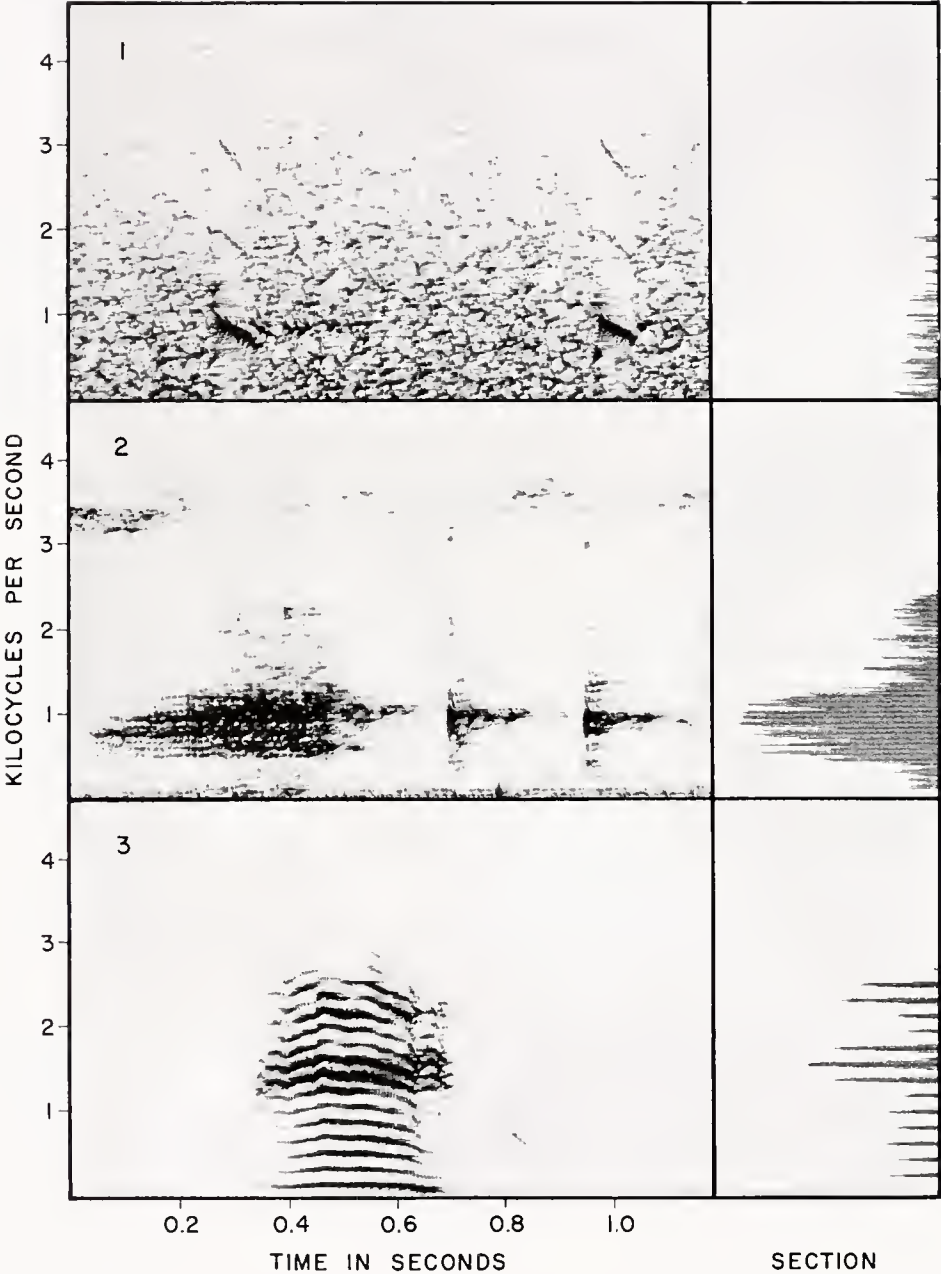


1. *Pternohyla fodiens*. 2. *Triprion spatulatus reticulatus*. 3. *Triprion petasatus*.

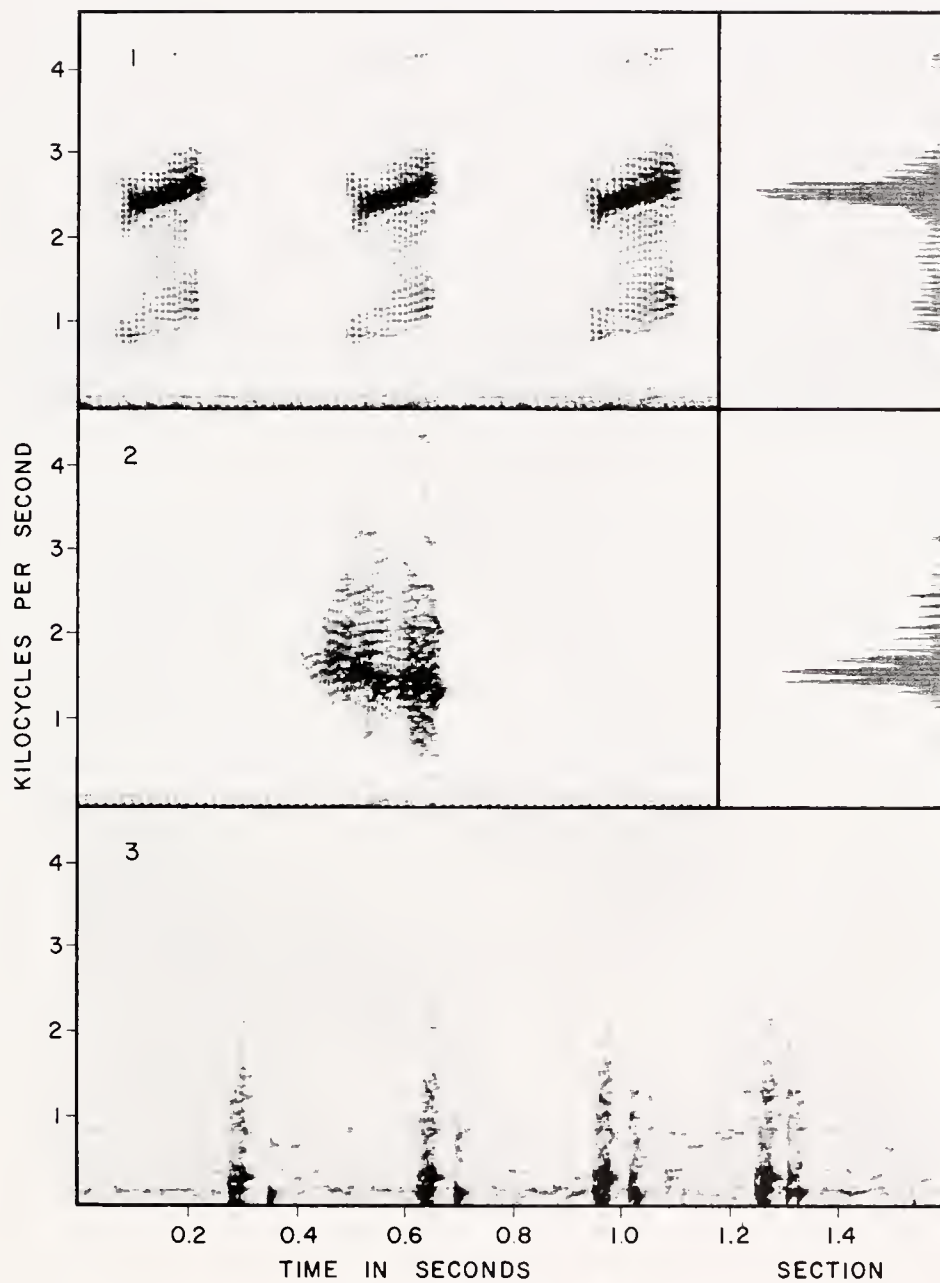




1. *Acris crepitans*. 2. *Phyllomedusa lemur*. 3. *Plectrohyla ixil*.

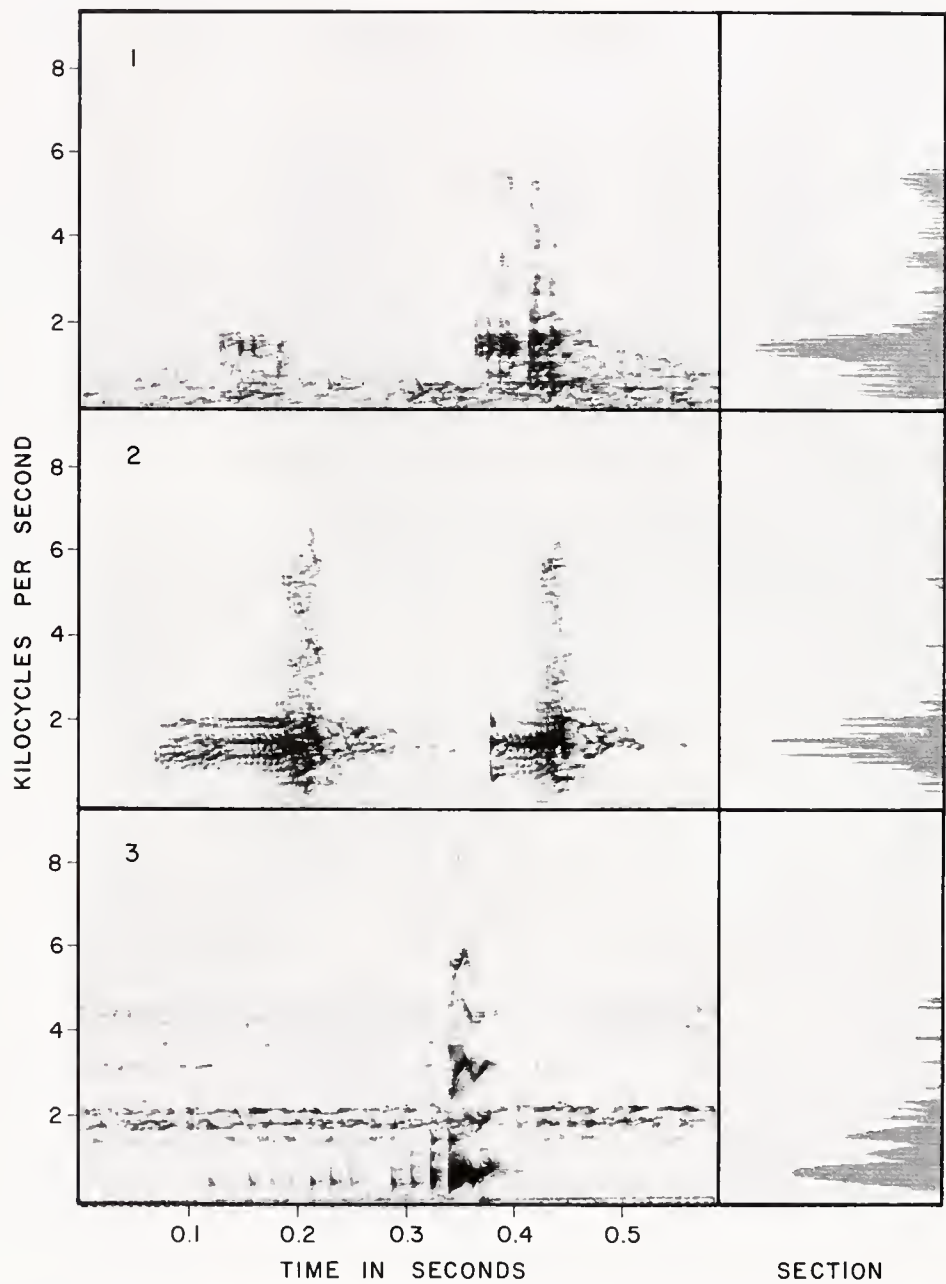


1. *Gastrotheca ceratophrys*. 2. *Gastrotheca nicefori*. 3. *Phrynohyas venulosa*.

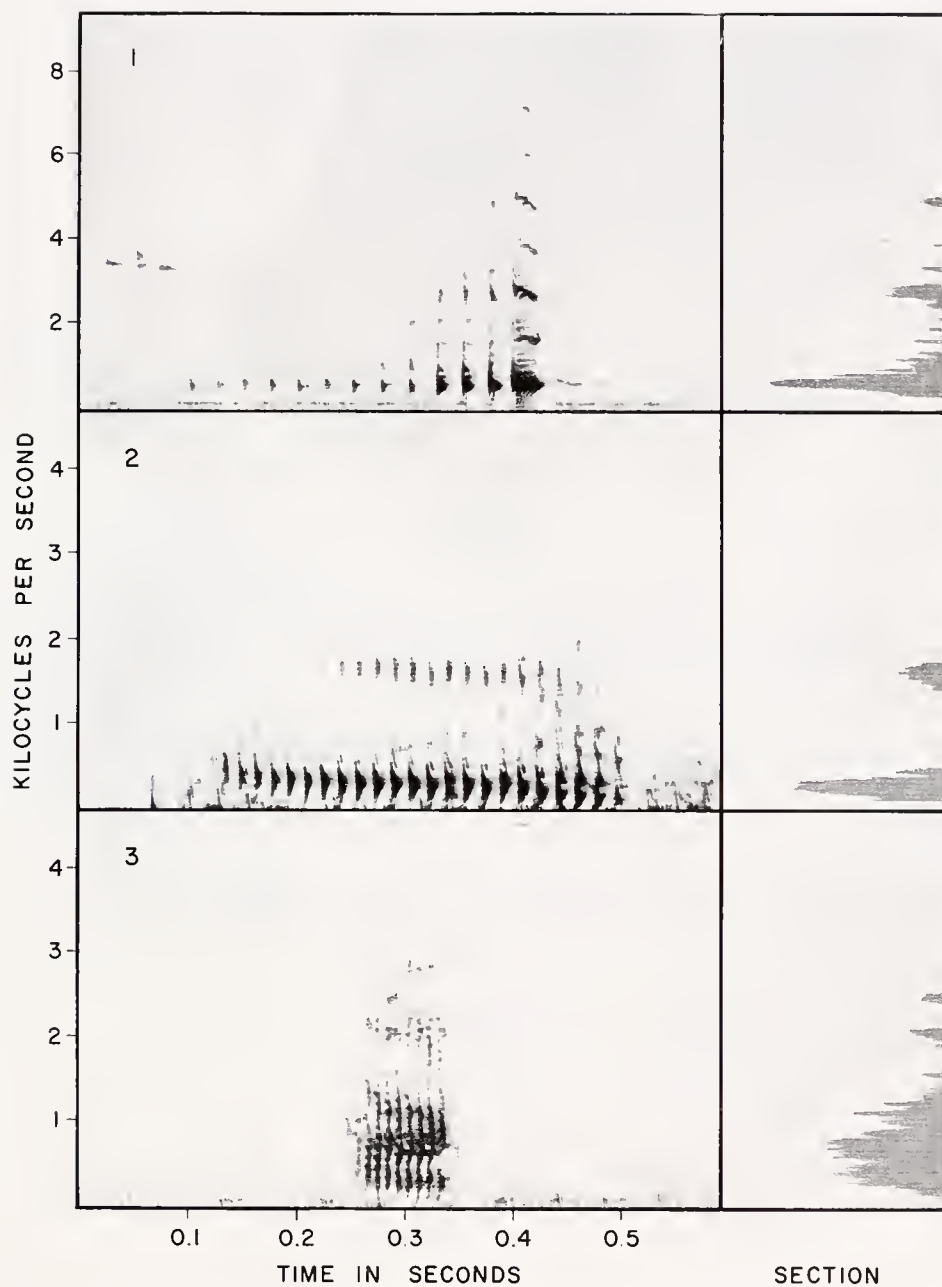


1. *Pseudacris clarkii*. 2. *Pachymedusa dacnicolor*. 3. *Phyllomedusa venusta* (release call).

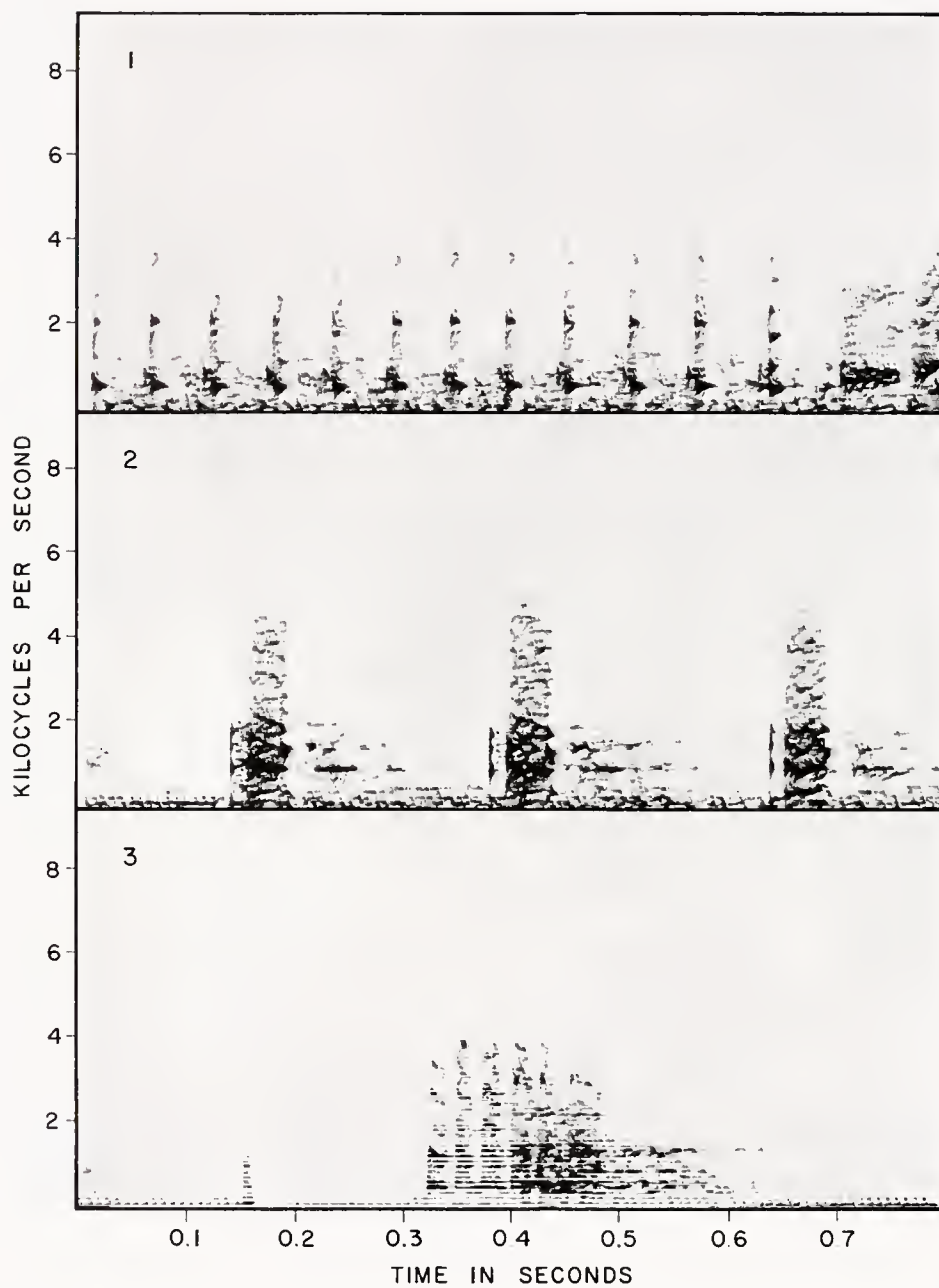




1. *Agalychnis saltator*. 2. *Agalychnis callidryas*. 3. *Agalychnis moreletii*.



1. *Agalychnis annae*. 2. *Agalychnis spurrelli*. 3. *Agalychnis litodryas*.



1. *Pachymedusa dacnicolor*. 2. *Smilisca baudinii*. 3. *Pternohyla fodiens* (all release calls).





1. *Pachymedusa dacnicolor*. 2. *Phyllomedusa venusta*.  $\times 1.5$ .





1. *Agalychnis saltator* (night). 2. *Agalychnis callidryas*. 3. *Agalychnis calcarifer*. 4. *Agalychnis saltator* (day). 5. *Agalychnis callidryas*.  $\times 1.5$ .







1. *Agalychnis moreletii*. 2. *Phyllomedusa lemur* (night). 3. *Agalychnis annae*. 4. *Agalychnis litodryas*. 5. *Phyllomedusa lemur* (day). 6. *Agalychnis spurrelli*.  $\times 1$ .







1. *Hyla miliaria*. 2. *Hemiphractus panamensis*. 3. *Anotheca spinosa*.  $\times 1.5$ .





1. *Gastrotheca nicefori*. 2. *Gastrotheca ceratophrys*.  $\times 1.5$ .



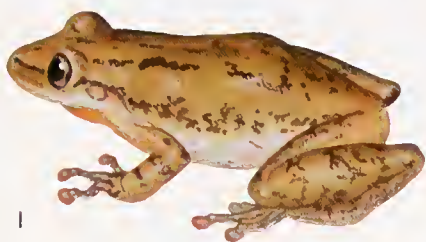




1-4. *Phrynohyas venulosa*.  $\times 1$ .







1, 2. *Hyla staufferi staufferi*. 3. *Hyla staufferi altae*. 4. *Hyla rubra*. 5, 6. *Hyla elaeochroa*.  $\times 2$ .





1, 2. *Hyla boulengeri*. 3. *Hyla rostrata*.  $\times 2$ .







1. *Hyla microcephala microcephala*. 2. *Hyla microcephala underwoodi*. 3. *Hyla robertmertensi*.  
4. *Hyla phlebodes*. 5. *Hyla sartori*. 6. *Hyla subocularis*. 7, 8. *Hyla ebraccata*.  $\times 2$ .







1. *Hyla rufitela*. 2. *Hyla crepitans*. 3. *Hyla boans* juvenile. 4. *Hyla rosenbergi*.  $\times 1.5$ .





1



2

1, 2. *Hyla boans*.  $\times 1$ .







1. *Hyla picadoi*. 2. *Hyla colymba*. 3. *Hyla angustilineata*, adult. 4. *Hyla angustilineata*, juvenile. 5. *Hyla pseudopuma pseudopuma*. 6. *Hyla pseudopuma infucata*.  $\times 2$ .







1. *Hyla tica*. 2. *Hyla rivularis*. 3. *Hyla debilis*. 4. *Hyla xanthosticta*. 5. *Hyla pictipes*, ♂.  
6. *Hyla pictipes*, ♀.  $\times 2$ .





1. *Hyla rufoculis*. 2. *Hyla lancasteri*, lowlands. 3. *Hyla uranochroa*. 4. *Hyla lancasteri*, Cerro Pando. 5. *Hyla legleri*.  $\times 2$ .







1, 2. *Hyla smithii*. 3. *Hyla godmani*. 4. *Hyla picta*. 5. *Hyla loquax*.  $\times 2$ .







1-4. *Hyla miotympanum*. 5. *Hyla erythromma*.  $\times 2$ .





1. *Hyla hazelae*. 2. *Hyla thorectes*. 3, 4. *Hyla arborescandens*. 5. *Hyla valancifer*, juvenile.  $\times 2$ .







1. *Hyla melanomma melanomma*. 2. *Hyla melanomma bivocata*. 3, 4. *Hyla pinorum*. 5. *Hyla mixomaculata*. 6. *Hyla pellita*. 7. *Hyla pinorum*, juvenile. 8. *Hyla nubicola*.  $\times 2$ .







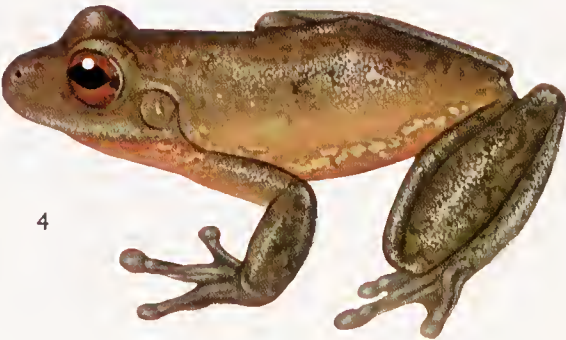
1



2



3



4



5



6

1, 2. *Hyla sumichrasti*. 3. *Hyla smaragdina*. 4. *Hyla salvadorensis*. 5. *Hyla bromeliacia*. 6. *Hyla dendroscarta*.  $\times 2$ .





1. *Hyla altipotens*. 2. *Hyla chaneque*, ♂. 3. *Hyla chaneque*, ♀.  $\times 1.5$ .







1. *Hyla taeniopus*, ♂. 2. *Hyla taeniopus*, ♀. 3. *Hyla altipotens*.  $\times 1.5$ .







1, 2. *Hyla bistincta*. 3, 4. *Hyla pentheter*.  $\times 1.5$ .





1. *Hyla charadricola*. 2. *Hyla chryses*. 3. *Hyla robertsoni*. 4. *Hyla siopela*, juvenile. 5. *Hyla siopela*, ♂.  $\times 1.5$ .







1



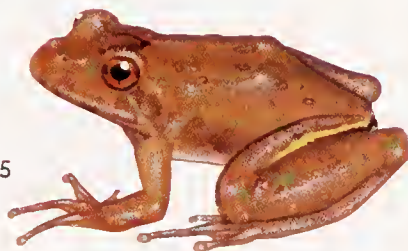
2



3



4



5

1. *Hyla cadaverina*. 2, 3. *Hyla arenicolor*. 4. *Pseudacris clarkii*. 5. *Acris crepitans*.  $\times 2$ .







1-4. *Hyla regilla hypochondriaca*. 5. *Hyla eximia*.  $\times 2$ .





1. *Hyla eximia*. 2. *Hyla plicata*. 3. *Hyla eximia*. 4, 5. *Hyla walkeri*. 6. *Hyla euphorbiacea*.  $\times 2$ .







1. *Ptychohyla schmidtorum schmidtorum*. 2. *Ptychohyla schmidtorum chamulae*. 3. *Ptychohyla ignicolor*. 4. *Ptychohyla euthysanota euthysanota*. 5. *Ptychohyla euthysanota macrotympanum*. 6. *Ptychohyla leonhardschultzei*. 7. *Ptychohyla spinipollex*.  $\times 2$ .







1. *Plectrohyla matudai*. 2. *Plectrohyla ixil*. 3. *Plectrohyla sagorum*. 4. *Plectrohyla quecchi*.  
× 2.





1. *Plectrohyla glandulosa*, ♂. 2. *Plectrohyla glandulosa*, ♀. 3. *Plectrohyla guatemalensis*.  
4. *Plectrohyla avia*.  $\times 1$ .







1, 2. *Smilisca phaeota*. 3. *Smilisca cyanosticta*. 4, 5. *Smilisca baudinii*.  $\times 1$ .







1, 2. *Smilisca sordida*. 3, 4. *Smilisca sila*. 5. *Smilisca puma*.  $\times 1.5$ .





1. *Triprion petasatus*. 2. *Triprion spatulatus reticulatus*. 3. *Triprion spatulatus spatulatus*.  
4. *Pternohyla fodiens*. 5. *Pternohyla fodiens*, juvenile.  $\times 1$ .











Date Due

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